RESEARCH ARTICLE

Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics

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Abstract

1. Body mass is a key life-history trait in animals. Despite being the largest animals on the planet, no method currently exists to estimate body mass of free-living whales.

2. We combined aerial photographs and historical catch records to estimate the body mass of free-living right whales (Eubalaena sp.). First, aerial photogrammetry from unmanned aerial vehicles was used to measure the body length, width (lateral distance) and height (dorso-ventral distance) of free-living southern right whales (Eubalaena australis; 48 calves, seven juveniles and 31 lactating females). From these data, body volume was estimated by modelling the whales as a series of infinitely small ellipses. The body girth of the whales was next calculated at three measurement sites (across the pectoral fin, the umbilicus and the anus) and a linear model was developed to predict body volume from the body girth and length data. To obtain a volume-to-mass conversion factor, this model was then used to estimate the body volume of eight lethally caught North Pacific right whales (Eubalaena japonica), for which body mass was measured. This conversion factor was consequently used to predict the body mass of the free-living whales.

3. The cross-sectional body shape (height–width ratio) of the whales was slightly flattened dorso-ventrally at the anterior end of the body, almost circular in the mid region, and significantly flattened in the lateral plane across the posterior half of the body. Compared to a circular cross-sectional model, our body mass model incorporating body length, width and height improved mass estimates by up to 23.6% (mean = 6.1%, SD = 5.27). Our model had a mean error of only 1.6% (SD = 0.012), compared to 9.5% (SD = 7.68) for a simpler body length-to-mass model. The volume-to-mass conversion factor was estimated at 754.63 kg/m³ (SD = 50.03). Predicted body mass estimates were within a close range of existing body mass measurements.
1 | INTRODUCTION

Body mass is a key life-history trait in animals (Schmidt-Nielsen, 1984). The mass of an animal will influence not only its metabolic rate and food requirements (Kleiber, 1947), but also its growth (Calder, 1982), fasting endurance (Millar & Hickling, 1990), thermoregulation (Porter & Kearney, 2009), foraging capacity (Brose, 2010), home range size (McNab, 1963), locomotion and cost of transport (Garland, 1983; Irschick & Higham, 2016). Body mass therefore constitutes a fundamental component in studies of animal physiology and bioenergetics (Peters, 1983).

Baleen whales are the largest animals on the planet, ranging from the 6.5 m and 3,500 kg pygmy right whale (Caperea marginata) to the 33 m and 190,000 kg blue whale (Balaenoptera musculus; Lockyer, 1976). Their large body size reduce their mass-specific metabolic rate and allows them to store large amounts of energy reserves to survive periods of low resource availability, which in turn enables them to undertake long distance migrations to exploit spatially and temporally clustered food resources (Brodie, 1975; Lockyer, 1981). Larger size in baleen whales is also correlated with foraging efficiency (Goldbogen et al., 2012; Goldbogen & Madsen, 2018), diving capacity (Mori, 2002; Noren & Williams, 2000) and relative cost of reproduction (Christiansen et al., 2018; Lockyer, 1981). Although it is one of their fundamental characteristics, body mass is seldom included in studies in baleen whales due to the difficulty of directly measuring this variable in the field.

Most existing data on body mass in baleen whales comes from dead animals, either caught in whaling operations (Lockyer, 1976, 1981; Lockyer & Waters, 1986; Omura, Ohsumi, Nemoto, Nasu, & Kasuya, 1969; Vikingsson, 1995) or from accidental fisheries bycatch or strandings (Fortune et al., 2012; Moore, Knowlton, Kraus, McLeilian, & Bonde, 2004). Working with dead specimens however has several limitations. Lethal sampling does not allow longitudinal studies of individuals (repeated sampling of the same individual over time), is not a viable method for small or vulnerable populations and is considered unethical by most nations (Aron, Burke, & Freeman, 2000). For stranding and bycatch data, samples can be biased towards animals in certain body conditions, age and/or reproductive classes (Moore & Read, 2008), whereas morphometric measurements can be distorted due to handling of the carcass or significant bloating or deflation of the body (Barratclough et al., 2014; Moore et al., 2004). Hence, it is necessary to develop non-invasive methods that can accurately estimate the body mass of free-living whales. While several studies have produced models to calculate body mass from length data (Fortune et al., 2012; Lockyer, 1976; Moore et al., 2004; Omura et al., 1969), these models do not take into account variations in the body condition of the animals. Most baleen whale species are capital breeders, and undergo large seasonal and annual fluctuations in their body condition, which can exceed 25% of their body mass (Christiansen et al., 2018; Lockyer, 1981; Vikingsson, 1995). Hence, body mass models need to incorporate both the structural size (i.e. body length) and the body condition of individual whales. Although attempts have been made to incorporate body condition into body mass models (Barratclough et al., 2014; Lockyer & Waters, 1986; Vikingsson, 1995), these either rely on body girth data, which cannot be obtained non-invasively from free-living whales, or assumed a circular cross-sectional body shape when converting body width to girth.

In this study we present an approach to accurately predict the body mass of free-living large whales, using non-invasive unmanned aerial vehicle (UAV) photogrammetry (Christiansen, Dujon, Sprogis, Arnould, & Beijer, 2016; Christiansen et al., 2018) and historical catch records (Omura et al., 1969). First, we measured the body length, width (lateral distance) and height (dorso-ventral distance) of free-living southern right whales (Eubalaena australis) from UAV images. We then developed a model to predict the body volume of the whales, which incorporated both their structural size (i.e. body length) and body condition (i.e. width and height). To test the performance of the model, we predicted the body volume of eight North Pacific right whales (Eubalaena japonica) caught in scientific whaling operations (Omura et al., 1969), for which the body mass was measured. From these predictions, we obtained a body volume-to-mass conversion factor, which we then used to calculate the body mass of the free-living whales measured by aerial photogrammetry. In addition to providing a method for estimating body volume and mass, our below method also provides a means to create accurate 3D models of whales, or other marine animals photographed in a similar manner, for use in computational fluid dynamics, or for use in Virtual Reality or Augmented Reality environments, such as for educational software.
2 MATERIALS AND METHODS

2.1 Measuring length, width and height of free-living whales

Aerial photogrammetry methods (Christiansen et al., 2016, 2018) were used to measure the body shape of southern right whales in Peninsula Valdés, Argentina (42°35′S, 64°33′W). A DJI Inspire 1 Pro quadcopter UAV (56 cm diameter, 3.4 kg, www.dji.com) equipped with a DJI Zenmuse X5 micro four-thirds camera (16 megapixel) with a 25 mm f1.8 lens (Olympus M.Zuiko) was flown from various vantage points on land and from a 5-m zodiac at sea to photograph the whales from an altitude of 20–40 m. The camera was facing directly down (using a camera gimbal), and images were captured as the whales displayed either their dorsal surface or lateral side at the surface.

From the dorsal photographs the total body length (BL, distance from tip of rostrum to the end of tail notch) and the width (W) of the whales at 5% increments along the body axis were extracted (Figure 1a). From the lateral photographs, the body height (H, dorso-ventral distance) was extracted at the same 5% intervals along the body axis (Figure 1b). All measurements were converted from pixels to metres by multiplying the relative size of the whale in the photograph with the camera sensor size and multiplying it with the ratio of the altitude of the UAV (measured using a Lightware SF11/C laser range finder mounted at the back of the UAV) and the focal length (Christiansen et al., 2018). The accuracy of the laser range finder was tested by Christiansen et al. (2018), who measured a known sized object on land at altitudes ranging from 5 to 120 m. Their results showed that within the altitude range used in this study (20–40m) the mean measurement error was 0.7 cm (SD = 0.5, n = 50) with a maximum of 1.6 cm.

Each measured whale was individually identified, using the unique callosity pattern on their heads (Payne et al., 1983), and classified into one of four reproductive classes: calf, juvenile, adult (non-pregnant or lactating) and lactating. Calves and lactating whales were classified based on their close association with each other, whereas juveniles and adults were separated based on their body length, using a body length threshold of 12 m, based on the smallest lactating female measured in this study. Only whales for which both body width and height estimates had been obtained were analysed.

2.2 Determining the cross-sectional body shape of whales

Few studies have investigated the cross-sectional body shape of baleen whales (Lockyer, McConnell, & Waters, 1985; Williamson, 1972), and as a consequence often a circular body shape is assumed (Christiansen, Vikingsson, Rasmussen, & Lusseau, 2013; Christiansen et al., 2018; Lockyer & Waters, 1986; Watts, Hansen, & Lavigne, 1993). With the aim of obtaining a more representative cross-sectional body shape of the whales, we calculated the ratio between the body height and width at each measurement site (Figure 1a). Using linear models in R (R Core Team, 2019), we investigated if the height-width (HW) ratio varied between reproductive classes (calf, juvenile, adult and lactating), and as a function of body length and condition (represented by the relative body width at 55%BL from the rostrum) within each reproductive class. Separate models were run for each measurement site (each HW ratio estimate).

The body width and height data were also used to create a representative 3D model of a right whale (Figure 1c), using the open source software Blender 3D (blender.org). Reference photos were also used to create taxonomic features (fluke, pectoral fins, eyes and mouth) onto the ellipsoid using Blender 3D sculpting tools (primarily the dynamic topology function). The model provides a taxonomically accurate depiction of a general right whale shape. A link to the right whale model on the Digital Life Project (www.digitallife3d.org) Sketchfab site is provided here: https://sketchfab.com/3d-models/
To capture the true body shape of the whales, we calculated the body mass from the body volume of the free-living southern right whales from the body length, width and height measurements. Across body variation in HW ratios were incorporated by modelling the whale’s cross-sectional shape as an infinite number of ellipses between each two adjacent width/height measurement sites, or segment (\(s\)). The volume, \(V\), for each body segment \(s\) for each individual \(i\) was given by the following equation:

\[
V_{ij} = BL_i \times 0.05 \times \int_0^1 \pi \times \frac{W_{A,i} + (W_{P,i} - W_{A,i})x}{2} \times \frac{H_{A,i} + (H_{P,i} - H_{A,i})x}{2} dx
\]

where \(BL_i\) is the total body length of whale \(i\), \(W_{A,i}\) and \(H_{A,i}\) are the anterior width and height measurements of body segment \(s\) for individual \(i\) and \(W_{P,i}\) and \(H_{P,i}\) are the posterior width and height measurements of segment \(s\) for individual \(i\) respectively. The equation to the right of the integral is equivalent to the area of an ellipse (\(A = \pi \times r_1 \times r_2\)), where \(r_1\) represent the major radius (semi-major axis), which is given by the first quotient, and where \(r_2\) represent the minor radius (semi-minor axis), which is given by the second quotient.

The end points of the whales (0 and 100%BL from the rostrum) were given a height and width of 0 m. To capture the gradual decrease in width and height towards the end of the tail region of the whales (>85%BL from the rostrum, see Figure S1), the height and width measurements at 90 and 95%BL from the rostrum were replaced by calculated values based on linear interpolation between the 85 and 100%BL measurement sites. The total volume, \(V_{\text{Total},i}\), of whale \(i\) was then obtained by calculating the sum of the volumes of all body segments \(S = 20\) in total:

\[
V_{\text{Total},i} = \sum_{j=1}^{20} V_{ij}
\]

### Converting body volume to body mass

Few measurements of body mass exist for right whales. Omura et al. (1969) obtained detailed measurements of body morphometrics and mass of 11 North Pacific right whales (\(E.\ \text{japonica}\)) caught during their summer feeding season in scientific whaling operations between 1961 and 1968, a population which is now endangered (Cooke & Clapham, 2018). Measurements included body mass (to the nearest kilogram, not including the weight of blood and other body fluids lost during the processing of the carcass), total body length (to the nearest decimetre) and half girths (to the nearest centimetre) measured at three locations: the anterior insertion of the pectoral fins (at ~25%BL from the rostrum), across the umbilicus (at ~50%BL from the rostrum) and across the anus (at ~72%BL from the rostrum; Figure 1b; Omura et al., 1969). Three of the whales (all caught in 1961) showed large errors in their morphometric data, and were consequently removed. The remaining dataset comprised eight individuals, consisting of five immature whales (three males and two females), one mature male and two pregnant females, ranging in body length from 12.6 to 16.4 m (mean = 15.1 m, SD = 1.26) and in body mass from 28,917 to 78,499 kg (mean = 57,596 kg, SD = 16,330; for the full dataset used from Omura et al., 1969, see Table S1). The relative mass of the foetuses of the two pregnant females constituted less than 1% of maternal mass and where hence ignored. The whales were caught between the 20 July and the 10 August, with prey items (\(\text{Calanus}\) sp.) in their stomachs and intestine (Omura et al., 1969).

To determine the relationship between body volume and mass for right whales, the width and height data from the free-living southern right whales were first used to estimate the girth of the whales at the same three measurements sites (the anterior insertion of the pectoral fin, the umbilicus and the anus) as in Omura et al. (1969), using the complete elliptic integral of the second kind formula to calculate the circumference (i.e. body girth, \(G\)) of an ellipse (Byrd & Friedman, 2013):

\[
G_i = 4 \times \pi \times \sqrt{r_{W,i}^2 \times \cos^2 (x) + r_{H,i}^2 \times \sin^2 (x)}
\]

where \(r_{W,i}\) represent the radius of the body width (\(W\)) and \(r_{H,i}\) represent the radius of the body height (\(H\)) of whale \(i\) at the position of the girth measurement (i.e. 25, 50 or 72%BL from the rostrum).

Linear models in \(x\) were then used to model the body volume, \(V_r\), of whale \(i\) as a function of its measured body length (\(BL_i\)) and estimated girths at the pectoral fin (\(G_{25\%BL,i}\)), the umbilicus (\(G_{50\%BL,i}\)) and the anus (\(G_{72\%BL,i}\)). All variables were log transformed to account for the nonlinear relationship between variables:

\[
\log (V_i) = a + \beta_1 \times \log (BL_i) + \beta_2 \times \log (G_{25\%BL,i}) + \beta_3 \times \log (G_{50\%BL,i}) + \beta_4 \times \log (G_{72\%BL,i})
\]

Although a high collinearity between the explanatory variables was expected (Figure S2), this did not affect the predictive power of the model and we therefore kept all the variables in the model. The resulting model parameters were then used to predict the body volume of the dead whales measured by Omura et al. (1969), using the published body length and girth measurements reported in the manuscript. A body volume-to-mass conversion factor was then calculated for the dead whales by dividing their measured body mass with their predicted body volume from the model. Using this conversion factor, we then predicted the body mass of the free-living southern right whales measured by aerial photogrammetry in Argentina from their estimated body volumes.

### Model accuracy

Using the same approach as for body volume, we used linear models to predict the body mass, \(M_i\), of whale \(i\) as a function of its measured body length (\(BL_i\)) and estimated girths at the pectoral fin (\(G_{25\%BL,i}\)), the umbilicus (\(G_{50\%BL,i}\)) and the anus (\(G_{72\%BL,i}\)) (Model 1):
\[
\log(M_i) = b_1 \times \log(BL_i) + b_2 \times \log(G_{25\%BL}) + b_3 \times \log(G_{50\%BL}) + b_4 \times \log(G_{75\%BL})
\]  
(5)

For comparison, we also created a predictive model of body mass as a function of body length (BL) alone (Model 2):
\[
\log(M_i) = b_1 \times \log(BL_i)
\]  
(6)

We also compared our model to that of Barratclough et al. (2014), which predicted the body mass of North Atlantic right whales (Eubalaena glacialis) based on their body length (BL) and their predicted circular body girth at 40%BL from the rostrum (\(C_{40\%BL}\)) (Model 3):
\[
M_i = 6,044.79 - 1.788 \times BL_i - 914 \times C_{40\%BL} + 500 \times BL_i \times C_{40\%BL}
\]  
(7)

where \(C_{40\%BL}\) is the predicted body girth of whale \(i\) at 40%BL from the rostrum, assuming a circular cross-sectional body shape where girth is estimated from the corresponding width measurement (\(C_{40\%BL} = \pi \times W_{40\%BL}\); Barratclough et al., 2014).

Next, we compared our model to that of Christiansen et al. (2018), which estimated the body volume of southern right whales by modeling their bodies as a series of truncated cones, attached to each other at each multiple measurement site. The approach however, assumed a circular cross-sectional shape of the whale, which did not take into account across body variations in HW ratios of the animals. The estimated body volume estimates from Christiansen et al.'s (2018) model was converted to body mass simply by multiplying the total volume obtained with the volume-to-mass conversion factor (Model 4):
\[
M_i = \sum_{s=1}^{S} V_{\text{Circular},s} \times D, V_{\text{Circular},s} = \frac{1}{3} \pi \times BL_i \times 0.05 (r_i^2 + R_i + R_i^2)
\]  
(8)

where \(D\) is the volume-to-mass conversion factor (i.e. overall body density), \(r_i\) is the radius of the anterior girth estimate (\(r_i = W_{A,i}/2\)) and \(R_i\) is the radius of the posterior girth estimate (\(R_i = W_{P,i}/2\)) for whale \(i\) (Christiansen et al., 2018).

Finally, we developed a fifth model (Model 5) to predict the body mass of the whales, using our elliptical body volume approach (Equations 1 and 2) and the estimated volume-to-mass conversion factor (\(D\)). To estimate the elliptical body volume of the whales, the measured body length (BL) and width (\(W_i\)) data were used, however, body heights (\(H\)) were predicted from the corresponding body widths (\(W\)) using the estimated HW ratios (full script in \(s\) available in Data S1; Model 5):
\[
M_i = \sum_{s=1}^{S} V_{\text{Elliptical},i} \times D, V_{\text{Elliptical},i} = \text{Equation 1 (Input data: BL, W and H [H predicted from W])}
\]  
(9)

The rationale of developing this approach (Model 5) was to be able to directly estimate the body mass of whales from their measured body length and width only, since body height is not always possible to measure in the field (i.e. it requires the whale to roll on its side).

To compare the accuracy of the five body mass models, we calculated the relative error in body mass (\(E_{M,i}\)) between our predictive models (\(M_{\text{predicted},i}\), i.e. models 1-5) and the estimated body mass (\(M_{\text{estimated},i}\)) of each whale \(i\):
\[
E_{M,i} = \frac{M_{\text{estimated},i} - M_{\text{predicted},i}}{M_{\text{estimated},i}}
\]  
(10)

where \(M_{\text{estimated},i}\) was estimated using the elliptical body volume model (Equations 1 and 2) and the measured body length, width and height (not predicted) of each whale, multiplied by the volume-to-mass conversion factor (\(D\)):
\[
M_{\text{estimated},i} = \sum_{s=1}^{S} V_{\text{Elliptical},i} \times D, V_{\text{Elliptical},i}
\]  
(11)

Relative body mass errors (\(E_{M,i}\)) were compared across body mass, reproductive classes, body length and body condition (body width at 55%BL from rostrum).

### RESULTS

#### 3.1 Sample size

We obtained aerial photographs of both the dorsal surface and lateral side of 102 southern right whales in Argentina between the 4 August and the 3 November, 2018. Photographs were taken by the UAV at altitudes ranging from 19.4 to 38.7 m (mean = 27.2 m, SD = 3.72). After removing duplicate individuals and animals with missing range finder data, a total of 86 whales remained. Of these, 48 were calves (BL = 4.31–8.22 m), seven juveniles (BL = 9.26–11.88 m) and 31 lactating females (BL = 12.83–15.05 m; Figure S3, Table S2).

**FIGURE 2** The body shape of southern right whales, measured as the height-width (HW) ratio across the body from 5% to 85%BL from the rostrum (see Figure 1 for location of measurement sites). The different reproductive classes are indicated by the colours of the filled data points (see colour legend). The solid black line represents the average HW ratio of all reproductive classes. The dashed black line indicates a ratio of 1:1, equivalent to a circular body shape. Significant differences in HW ratios between reproductive classes for each measurement site are indicated with red asterisks (*). \(N = 48\) calves, seven juveniles and 31 lactating females.
3.2 | Cross-sectional body shape of southern right whales

The HW ratio varied considerably along the body axis of the whales (Figure 2). From the rostrum down to approximately 35%BL from the rostrum, the body shape was flattened in the dorso-ventral plane, with a HW ratio between 0.847 and 0.953 (Figure 2, Table S3).

Around the middle of the body, between 40% and 50%BL from the rostrum, the HW ratio was close to one, suggesting a near circular body shape (Figure 2, Table S3). Posterior to 50%BL from the rostrum the body shape became increasingly flatter in the lateral plane, with a HW ratio ranging from 1.090 to 1.928 (Figure 2, Table S3).

There was a significant difference between reproductive classes in HW ratio for most measurement sites (Figure 4, Table S3), with calves being more slender in the lateral plane across most of their bodies (30%–75%BL from the rostrum) compared to lactating females, apart from at the very end of the peduncle (85%BL from the rostrum), where lactating females and juveniles had a higher HW ratio.

The body length of the whales did not influence their HW ratio. Furthermore, their relative body condition (i.e. body width at 55%BL from the rostrum) did not influence the body shape of juveniles or lactating females. The body shape of calves, however, changed significantly as a function of body condition at all measurement sites between 25% and 80%BL from the rostrum, with the HW ratio decreasing at each site as body condition increased (Figure 3, Table S4).

3.3 | Body volume and mass of southern right whales

We obtained body volume estimates of southern right whales ranging from 1.45 to 55.56 m$^3$ (Table S2). The estimated girths of the 86 southern right whales, calculated from the width and height data in order

**FIGURE 3** The body shape of southern right whale calves (height-width ratio) across the body from 5% to 85%BL from the rostrum (see Figure 1 for location of measurement sites), as a function of their relative body condition (i.e. body width at 55%BL from the rostrum) (see colour legend). The dashed black horizontal line indicates a ratio of 1:1, equivalent to a circular body shape. N = 48 calves.

**FIGURE 4** Southern right whale body volume as a function of (a) body length (BL), (b) body girth at anterior insertion of the pectoral fin ($G_{25\%BL}$), (c) girth at the umbilicus ($G_{50\%BL}$) and (d) girth at the anus ($G_{72\%BL}$), on the log–log scale (see Figure 1b for location of measurement sites). The solid black lines represent the fitted regression lines from the linear models. The equation for each relationship can be found in the bottom-right corner of each sub-figure. The colour of the data points represent the different reproductive classes (see colour legend).
to relate body volume to mass, ranged from 2.30 to 9.22 m across the pectoral fin ($G_{25\%BL}$), from 2.76 to 9.28 m across the umbilicus ($G_{50\%BL}$) and from 1.69 to 6.81 m across the anus ($G_{72\%BL}$; Table S2). There was a positive relationship between all girth estimates on the log-log scale, as well as between girths and body length (Figure S2).

There was a strong relationship between the body volume ($V$) of southern right whales and their body length (BL, $F_{1,84} = 7,614, p < .001$, $R^2 = .989$) and girths at the pectoral fin ($G_{25\%BL}$, $F_{1,84} = 19,733, p < .001$, $R^2 = .996$), umbilicus ($G_{50\%BL}$, $F_{1,84} = 10,475, p < .001$, $R^2 = .992$) and anus ($G_{72\%BL}$, $F_{1,84} = 1836, p < .001$, $R^2 = .956$) on the log-log scale (Figure 4). The full predictive model for body volume included body length and all three body girth estimates ($F_{4,84} = 70,050, p < .001$) and explained 99.9% of the variance ($R^2$) in body volume:

$$
\log(V) = -2.764 + 1.003 \times \log(BL) + 0.809 \times \log(G_{25\%BL}) + 0.814 \times \log(G_{50\%BL}) + 0.294 \times \log(G_{72\%BL}). \tag{12}
$$

The mean relative body mass error of Model 1 (difference between Equations 13 and 11) was 1.6% ($SD = 0.012$), with a maximum error of 5.7% (Figure 6a). The errors were homogenous across body mass, reproductive classes, body length and body condition (relative body width at 55%BL from rostrum) (Figure 6a).

The predictive model of body mass as a function of body length (Model 2) was also significant ($F_{1,84} = 7,614, p < .001$) and explained 98.9% of the variance ($R^2$) in body mass:

$$
\log(M) = 2.696 + 2.938 \times \log(BL). \tag{14}
$$

As expected, the predicted model for body mass as a function of body length and the three girth estimates (Model 1, Equation 13) was identical to the body volume model (Equation 8; $F_{4,81} = 70,050$, $p < .001$, $R^2 = .999$), the only difference being the intercept parameter which had increased from $-2.764$ (Equation 12) to 3.862 (Equation 13), on the log-log scale, due to the multiplication with the volume-to-mass conversion factor:

$$
\log(M) = 3.862 + 1.003 \times \log(BL) + 0.809 \times \log(G_{25\%BL}) + 0.814 \times \log(G_{50\%BL}) + 0.294 \times \log(G_{72\%BL}). \tag{13}
$$

The mean relative body mass error of Model 1 (difference between Equations 13 and 11) was 1.6% ($SD = 0.012$), with a maximum error of 5.7% (Figure 6a). The errors were homogenous across body mass, reproductive classes, body length and body condition (relative body width at 55%BL from rostrum) (Figure 6a).

The model of Barratclough et al. (2014) (Model 3) had a mean body mass error (difference between Equations 7 and 11) of 17.4% ($SD = 14.07$) and a maximum of 70.7% (Figure 6c). Their model significantly underestimated body mass, especially for calves with low body mass and short body lengths (Figure 6c).

The circular cross-sectional model (Model 4), based on Christiansen et al. (2018), had a mean body mass error (difference

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**FIGURE 5** Predicted body mass ($M$) and volume of southern right whales (circular points, $N = 86$, Table S2) and North Pacific right whales (black crosses, $N = 8$, Omura et al., 1969, Table S1) as a function of body length (BL). The colour of the southern right whale data represents the different reproductive classes (top-left colour legend). The fitted lines represent the predicted body mass (left y-axis) and body volume (right y-axis) from body length estimated for southern right whales (solid black, this study), North Pacific right whales (dashed red, $M_i = 13.2 \times BL_i^{2.06}$, Lockyer, 1976) and North Atlantic right whales (dotted blue, $\log(M_i) = 2.94 + 2.82 \times \log(BL_i)$, Fortune et al., 2012) (bottom-right colour legend).
FIGURE 6  Relative error in body mass estimates (difference in predicted body mass and measured body mass) of southern right whales based on five models. (a) Body mass \( M \) predicted from body length (BL) and body girth at the pectoral fin \( G_{25\%BL} \), umbilicus \( G_{50\%BL} \) and anus \( G_{72\%BL} \) (Model 1). (b) \( M \) predicted from BL (Model 2). (c) \( M \) predicted from BL and circular girth at 40\%BL from rostrum \( C_{40\%BL} \) (Model 3, from Barratclough et al., 2014). (d) \( M \) estimated from circular body volume model (Model 4, from Christiansen et al., 2018) based on only BL and width (W) measurements multiplied with the volume-to-mass conversion factor \( 754.63 \text{ kg/m}^3 \). (e) \( M \) estimated from elliptical body volume model (Model 5) based on BL and W measurements, and predicted H (from W based on the known HW ratios), multiplied with the volume-to-mass conversion factor \( 754.63 \text{ kg/m}^3 \). Relative body mass errors for the five models were tested against body mass (first column), reproductive class (second column), body length (third column) and body condition (fourth column). Body condition was expressed as the relative body width of whales at 55\%BL from the rostrum. To facilitate comparison in model accuracy, the 0 (solid red line) and 5\% error range (dashed red lines) is highlighted. Juv. = Juvenile, Lac. = Lactating female. \( N = 86 \) whales.
between Equations 8 and 11) of 6.1% (SD = 5.27) and a maximum of 23.6%. The error was largest for calves in poor body condition (i.e., low relative width at 55%BL from the rostrum), due to their high HW ratio (Figure 6d).

Finally, the body mass predicted from our elliptical body volume model (where body height was predicted from body width based on the estimated HW ratios) and the body volume-to-mass conversion factor (Model 5) had a mean error (difference between Equations 9 and 11) of 5.4% (SD = 4.53) and a maximum of 19.0% (Figure 6e), with 25% of estimates being within 2.0%, 50% within 4.2% and 75% within 6.6% of the estimated body masses ($M_{\text{estimated}}$) of the whales (Figure 6e).

4 | DISCUSSION

This study demonstrates how aerial photogrammetry together with historical catch records can be used to measure the body mass of free-living whales. Our non-invasive approach using body length, width and predicted height (from the calculated HW ratios) produced body mass estimates with a high level of accuracy (Model 5 in Figure 6). With the mean measurement errors (mean = 5.4%, SD = 4.53) being considerably lower than the known seasonal variation in body condition of southern right whales (~25%, Christiansen et al., 2018), our body mass model is able to accurately capture both seasonal and annual variations in body mass of right whales. This would not be possible to detect with the alternative body length-to-mass model (Model 2 in Figure 6) or the model developed by Barratclough et al. (2014) (Model 3 in Figure 6), which had maximum errors exceeding the seasonal variation in body mass of right whales. Although this case study is focused on right whales, our body mass modelling approach can be applied to any species of marine mammal for which alternative methods (e.g., live capture) are not feasible or desirable. The script used in this study (Data S1) can be directly applied to other right whale populations world-wide, or be adjusted to other species by simply changing the input parameters.

Although the true body mass of the southern right whales measured in this study was unknown, our predicted estimates were similar to existing (measured) body mass data, and derived body length-to-mass models (based on actual measurements of body mass) for right whales in the North Atlantic (Fortune et al., 2012) and the North Pacific (Lockyer, 1976; Omura et al., 1969; Figure 5). The three models produced almost identical body mass estimates for calves from birth (1,076–1,147 kg at 4.3 m BL) to about 3 months of age (7,072–8,257 kg at 8.2 m BL; Figure 5). The juvenile and adult North Pacific right whales measured by Omura et al. (1969) had a slightly higher body mass compared to the estimated mass of southern right whales in Argentina (Figure 5), which was not surprising, considering the former were measured during their feeding season while the latter were estimated during the breeding season. The lower measured body mass of the North Atlantic right whales (Figure 5) is likely a reflection of their poorer body condition caused by high exposure to anthropogenic stressors (Knowlton, Hamilton, Marx, Pettis, & Kraus, 2012; Moore et al., 2004; Rolland et al., 2016).

Few studies have tried to describe the cross-sectional body shape of whales (Lockyer et al., 1985; Williamson, 1972). By photographing both their dorsal surface and their lateral side, we were able to show that the HW ratio of southern right whales varied considerably across their bodies (Figure 2). Lockyer et al. (1985) provided diagrammatic transverse sections through the body of fin (Balaenoptera physalus) and sei whales (Balaenoptera borealis) at numerous girth positions, showing a similar dorso-ventral flattening towards the posterior end of the whales’ bodies. Accounting for this variation in HW ratio of the whales significantly improved our body mass estimates by up to 23.6% (mean = 6.1%, SD = 5.27) compared to circular cross-sectional models (Christiansen et al., 2018). For juveniles and adults, the HW ratio remained constant across body length and condition, meaning that, once the HW ratios are known, only data on body length and width are needed to accurately calculate the body volume and mass of these reproductive classes. In contrast, the HW ratio of calves decreased (the cross-sectional body shape became more circular) with increased body condition, meaning that the body condition (i.e., absolute body width at 55%BL from rostrum) also needs to be incorporated when calculated body volume and mass of calves.

We obtained a volume-to-mass conversion factor, or average tissue density, of right whales of 754.63 kg/m$^3$ (SD = 50.03). This estimate does not take into consideration the relative proportion of different tissues comprising the body of the whale. Omura et al. (1969) measured the relative weight proportion of the different tissues in the same North Pacific right whales to be 40.2% blubber, 31.5% muscle, 13.5% bones and 13.2% visceral and organ tissue. Using these proportions in combination with published food densities (g/ml) from FAO (Blubber = 0.70, muscle = 0.96, bones = 0.72, visceral = 0.93, Charrondiere, Haytowitz, & Stadlmayr, 2012), we obtained a similar average tissue density of 803.76 kg/m$^3$. These estimates of tissue density suggest that right whales are positively buoyant, which corresponds with studies of tagged whales (Nowacek et al., 2001) and historical reports from whalers who found that right whales often floated after being killed (Starbuck, 1878). Given that the relative proportion of different tissues in baleen whales is known to vary seasonally (Lockyer, 1981; Vikingsson, 1995), it is possible that our body mass estimates for southern right whales is slightly biased since it is based on North Pacific right whales caught during their summer feeding season. Although the exact timing of the feeding season for North Pacific right whales remains unknown, the catch dates (20 July and the 10 August) appear to be somewhere in the middle of the season. Had the whales been measured at the very end of the feeding season, their relative fat content would likely have been higher, which would have resulted in a lower overall body density and volume-to-mass conversion factor. With the exception of calves, the opposite trend should be visible on the breeding grounds, with the overall body density of whales gradually increasing as their relative fat content decrease through the breeding season. The volume-to-mass conversion factor might also differ between reproductive classes as found by Lockyer (1981) for
fin whales, where mature and pregnant whales had a higher relative increase in visceral tissue compared to immature whales.

Body size is a fundamental aspect of the life history of baleen whales (Brodie, 1975; Christiansen et al., 2018; Goldbogen & Madsen, 2018; Lockyer, 1976, 1981). Due to their large size, baleen whales serve an important role in marine ecosystems, including the transfer of nutrients from high productive high-latitude feeding areas to low-latitude nutrient-poor breeding areas, and facilitates sequestration of carbon to deep sea habitats (Roman et al., 2014). The ability to estimate body mass of free-living whales will open up new avenues in several fields of research, including bioenergetics, ecophysiology and ecological energetics. From a conservation and management perspective, being able to directly assess the body mass of entangled and live-stranded whales that are unable to survive without intervention will facilitate more accurate sedative dosing (Barratclough et al., 2014). Finally, our methods can be used to create accurate 3D models of living whales and potentially other marine animals photographed in a similar manner. Obtaining accurate HW ratios is a key first step for developing realistic 3D models which can then be used for computational fluid dynamics analysis, or for use in virtual reality or augmented reality environments for educational use.

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Fieldwork.

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AUTHORS’ CONTRIBUTIONS

F.C. conceived and designed the study in collaboration with M.S., M.J.M. and M.M.U. F.C., M.S., M.J.M. and M.M.U. obtained funding for the fieldwork. F.C. conducted the fieldwork with logistic support from M.S., M.J.M., M.D.M., M.R. and M.M.U. F.C. and H.A.W. processed the data. F.C. analysed the data. R.G. and D.J.J. developed the 3D model. F.C. wrote the manuscript. All authors contributed to subsequent drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The R script used to estimate body mass (Data S1), as well as the raw data (Data S2) from this article can be found online in the Dryad Repository https://doi.org/10.5061/dryad.m0087p4 (Christiansen et al., 2019).

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SUPPORTING INFORMATION

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