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RESEARCH ARTICLE

Energy expenditure of southern right whales varies with body size, reproductive state and activity level

Fredrik Christiansen^{1,*}, Kate R. Sprogis², Mia L. K. Nielsen³, Maria Glarou⁴ and Lars Bejder⁵

ABSTRACT

Quantifying the energy expenditure of animals is critical to understanding the cost of anthropogenic disturbance relative to their overall energy requirements. We used novel drone focal follows (776 follows, 185 individuals) and aerial photogrammetry (5372 measurements, 791 individuals) to measure the respiration rate and body condition loss of southern right whales (*Eubalaena australis*) on a breeding ground in Australia. Respiration rates were converted to oxygen consumption rate and field metabolic rate (FMR) using published bioenergetic models. The intra-seasonal loss in body condition of different reproductive classes (calves, juveniles, adults, pregnant and lactating females) was converted to blubber energy loss and total energy expenditure (TEE). Using these two metrics, we tested the effects of body size, reproductive state and activity level on right whale energy expenditure. Respiration rates and mass-specific FMR decreased exponentially with an increase in body size, as expected based on allometric scaling. FMR increased curvilinearly with an increase in swim speed, probably as a result of increased drag and increased locomotion costs. Respiration rates and FMR were 44% higher for pregnant and lactating females compared with those of adults, suggesting significant costs of fetal maintenance and milk production, respectively. The estimated FMR of adults based on their respiration rates corresponded well with the estimated TEE based on body condition loss. The rate of decline in body condition of pregnant and lactating females was considerably higher than expected based on respiration rates, which probably reflects the milk energy transfer from mothers to calves, which is not reflected in their FMR.

KEY WORDS: Aerial photogrammetry, Baleen whale, Bioenergetics, Drones, Field metabolic rate, Total energy expenditure

INTRODUCTION


Animals require energy for maintenance, activity, somatic growth and reproduction (Brett and Groves, 1979; Kleiber, 1975). By studying energy expenditure across different life and reproductive stages, it is possible to infer the relative costs of these energetic components, and how they change over the lifetime of a species to maximize fitness (Perrin and Sibly, 1993; Stearns, 1989). Such a

quantitative framework for the energy expenditure of wild animals is critical for informed management and conservation efforts by numerically quantifying the costs of anthropogenic disturbance in relation to the overall energy requirements of an animal and hence ultimately vital rates and population dynamics (Christiansen and Lusseau, 2015; NRC, 2005; Villegas-Amtmann et al., 2017). Baleen whales include species that are the largest animals on the planet (Lockyer, 1976). Whales provide important ecosystem services by transporting nutrients between geographical areas and sequestering carbon to deep sea habitats through whale falls (Roman et al., 2014). These services make whales important marine ecosystem engineers that help maintain healthy ecosystems. To further assess their ecological importance, it is crucial to understand the prey consumption of baleen whales, for which knowledge of their energy expenditure is required.

Body size is one of the most important determinants of the energy requirements of animals (Kleiber, 1932; Peters, 1983). The energy needed for maintenance scales exponentially with body mass so that the mass-specific energy expenditure decreases with increased mass (Brody, 1968; Kleiber, 1932). The body size of baleen whales varies substantially, from the 6.5 m (3500 kg) pygmy right whale (*Caperea marginata*) to the 33 m (190 tonnes) blue whale (*Balaenoptera musculus*) (Lockyer, 1976). Even within species, there is a large size difference between newborn and adult animals (Lockyer, 1976). As mass-specific energy expenditure decreases with increased body size (Kleiber, 1932), the relative cost of maintenance should decline significantly with body length. Somatic growth also requires energy, with costs generally being highest at the early stages of life (Dmitriev, 2011; Douhard et al., 2017). Baleen whales grow rapidly during the first years of life, which should incur significant energetic costs (Christiansen et al., 2018, 2022b; Lockyer, 1984). These costs, however, should decline rapidly as the whale increases in size and ultimately reaches its asymptotic length. An individual's energy expenditure will also be influenced by its activity level as movement requires additional energy to be catabolized (Alexander, 2005; Halsey et al., 2009). Whales are exclusively marine, and hence need to spend energy to propel themselves through the relatively dense medium of water. Because the power to overcome drag increases with the cube of speed (Schmidt-Nielsen, 1997), the energy expenditure of whales should similarly increase with swim speed (Williams et al., 1993; Yazdi et al., 1999). Finally, reproduction often adds a significant energetic cost to animals, with the cost of individual reproductive events being particularly high for females of K-selected species, which invest a large amount of energy into a small number of offspring (Gittleman and Thompson, 1988; Oftedal, 1985). This is especially true for baleen whales, which have evolved some of the fastest offspring growth rates among mammals (Frazer and Huggett, 1959, 1973), with late pregnancy and lactation being considered the most energetically expensive components of their life cycle (Christiansen et al., 2018, 2022a; Lockyer, 1981a).

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Measuring the energy expenditure of baleen whales can be challenging, as conventional techniques (e.g. doubly labelled water method) are not feasible (Butler et al., 2004). Instead, because oxygen consumption is fundamentally driven by the respiration rate of cetaceans, it is possible to infer the field metabolic rate (FMR) of free-swimming cetaceans on short time scales from their respiration rate, if the tidal volume and oxygen extraction per breath are estimated correctly (Folkow and Blix, 1992; Rojano-Doñate et al., 2018; Yazdi et al., 1999). FMR represents the catabolized energy needed for maintenance and activity. On longer time scales, it is possible to infer the total energy expenditure (TEE) in baleen whales by measuring the temporal variations in their body condition (relative energy reserves) during periods of fasting (Christiansen et al., 2016a, 2020a; Lockyer and Waters, 1986). TEE represents both the catabolized (for maintenance and activity) and deposited energy of cetaceans, with the latter including energy for somatic growth, fat deposition and (for pregnant and lactating females) transfer to offspring. Many species of baleen whales make annual migrations between productive summer feeding grounds and oligotrophic winter breeding grounds (Kasuya, 1995; Lockyer, 2007). Whilst on their breeding grounds, whales rely almost exclusively on accumulated fat reserves from their previous feeding seasons. Only calves are provided with energy from their mothers in the form of milk. The rate of decline in body condition of whales (non-calves) on the breeding grounds should hence directly reflect their TEE.

The aim of this study was to determine the effect of body size, activity level and reproductive state on the energy expenditure of southern right whales (*Eubalaena australis*), a capital breeding mysticete. We combined unmanned aerial vehicle (UAV) focal follow (Nielsen et al., 2019a; Sprogis et al., 2020a) and aerial photogrammetry methods (Christiansen et al., 2016a, 2018) to measure the respiration rate, swim speed, body size and body condition of different reproductive classes (calves, juveniles, adults, pregnant and lactating females) of right whales on a breeding ground in South Australia. The respiration rate data were used to estimate the FMR of whales, while the intra-seasonal loss in body condition was used to calculate TEE. Using these metrics, we tested three hypotheses relating to size, activity and reproductive state of animals. In hypothesis I (body size), we predicted the respiration rate and mass-specific FMR of whales would decrease exponentially with increased body size. For hypothesis II (activity level), we expected the respiration rate and FMR of right whales to increase curvilinearly with an increase in swim speed. For hypothesis III (reproductive state), we expected pregnant and lactating females to have an overall higher respiration rate and FMR compared with non-pregnant/non-lactating (NPNL) adults. We also compared our estimates of FMR based on respiration rates with our TEE estimates obtained from the body condition data. We expected FMR and TEE to be similar for juveniles and NPNL adults, as maintenance and activity are the primary costs for these reproductive classes, which also should be captured by both metrics. For pregnant and lactating females, we expected TEE to be higher than FMR, as females transfer considerable amounts of energy to their offspring, which will not be reflected in their FMR. Finally, to provide a direct link between behaviour (i.e. respiration rate) and bioenergetics, we calculated the energetic cost per breath of right whales, to aid future studies assessing the effects of human disturbance on large baleen whales.

MATERIALS AND METHODS

Ethics statement

All research was conducted under scientific research permits from the Department for Environment and Water (DEW), South Australia

(M26501-2, M26501-4, M26501-5 and M26501-6); South Australian Marine Parks permits (MR00082-3-V, MO00082-4-R, MO00082-5-R and MO00082-6-R); and animal ethics permits from DEW (4/2016) and Murdoch University (O2819/16). UAVs were operated under UAV operator certificates with the necessary remotely piloted aircraft system licences in accordance with regulations by the Australian Civil Aviation Safety Authority.

Data collection

Study area

Behavioural and body morphometric data were collected from southern right whales, *Eubalaena australis* (Desmoulin 1822), at the Head of Bight (31°29'S, 131°08'E; Fig. 1) in South Australia between 24 June and 25 September 2016–2019. The Head of Bight constitutes a major breeding/calving ground for right whales from the 'western' Australian subpopulation, which currently numbers around 2500–3000 individuals (Smith et al., 2021). The Head of Bight is an open population and represents a relative proportion (0.21–0.48) of the overall south-western population (Charlton et al., 2022). Whales are present at the Head of Bight each year between May and October, with a peak in abundance between late June and mid-August (Burnell and Bryden, 1997; Charlton et al., 2019). Pregnant females generally arrive at the Head of Bight within a week or two of giving birth, which occurs between early May and late August, with a peak around 1 July (F.C., unpublished data). The number of days that these females have spent on the breeding grounds prior to arriving at the Head of Bight study area is unknown. The mean residency period for mother and calf pairs at the Head of Bight is 40 days, while unaccompanied adults and juveniles stay on average 14.7 days (Charlton, 2017). Mother–calf pairs maintain low energy budgets with shallow dives whilst on the breeding ground (generally <10 m; Nielsen et al., 2019b), and at Head of Bight, behaviours are representative of natural, undisturbed behaviours as there is a vessel exclusion zone that excludes anthropogenic disturbance (Nielsen et al., 2019a). The majority of whales at the Head of Bight reside within 2 km of the shore and within the 10 m depth contour (Charlton et al., 2019), thus making the Head of Bight an ideal location for land-based UAV sampling of right whale natural behaviours.

UAV focal follows

Behavioural focal follows of right whales were conducted using a DJI Phantom 3 Pro multicopter UAV (diameter without propellers: 35 cm, mass: 1.4 kg; www.dji.com) equipped with a 12.4 Megapixel camera with a 20 mm f/2.8 lens. Following the protocol of Nielsen et al. (2019a), the UAV was flown from multiple vantage points on land (Fig. 1) over a focal whale, where it remained for the duration of the battery and recorded video from an altitude of 20–100 m with the camera positioned vertically down. At this altitude, the underwater noise of the UAV is inaudible for right whales (Christiansen et al., 2016b), which have also been shown to not respond behaviourally to the presence of low-flying (<5 m) UAVs (Christiansen et al., 2020b). The UAV recorded video of the focal animal for up to 20 min per flight, and multiple flights were conducted over the same focal animal until the animal moved out of range of the study area or until the end of daylight hours. Flights were only conducted in calm weather conditions (wind speed <15 knots) and no precipitation. The GPS position of the UAV was recorded every 100 ms and was used to measure the movement of the focal animal by positioning the drone perfectly above it with the animal centred in the middle of the frame.

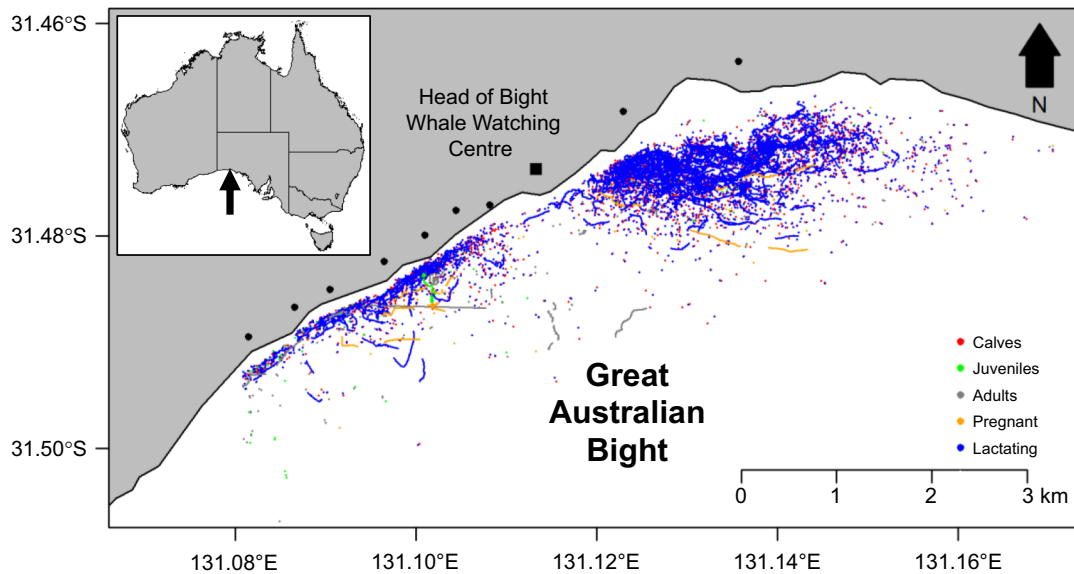


Fig. 1. The Head of Bight study area, South Australia. The locations of the unmanned aerial vehicle (UAV) photogrammetry measurements (coloured points) and focal follows (coloured lines) are shown. The colour key indicates the reproductive class of the sampled whales. The black points indicate the land-based vantage points used during the UAV sampling. The sample size for the UAV focal follows and UAV aerial photogrammetry sampling is presented in Tables 1 and 2, respectively. Note, flights were flown off the Head of Bight Whale Watching Centre after business hours only. The Whale Watching Centre represented land-based views from a cliff-top platform.

UAV aerial photogrammetry

A DJI Inspire 1 Pro multirotor UAV (diameter without propellers: 56 cm, mass: 3.4 kg; www.dji.com) with a 16 Megapixel Zenmuse X5 micro four-thirds camera with an Olympus M.Zuiko 25 mm f1.8 lens was used to take aerial photographs of right whales as they surfaced to breathe. To record the altitude of the UAV, a LightWare SF11/C laser range finder (LightWare Optoelectronics, mass: 35 g) was used. The UAV was flown at an altitude between 5 and 120 m above sea level and images were taken manually using an iPad Air. Pictures were taken of the dorsal side of the whales when they were close at the surface, with a straight body posture, a non-arching back and no rolling. The UAV was only flown during favourable weather conditions (no rain and wind speeds <15 knots). Following the protocol of Christiansen et al. (2018), all photographs were graded based on multiple criteria: camera focus, degree of body roll, degree of body arch, body pitch (vertically), body length measurability and body width measurability. The grading was done on a scale from 1 to 3, where 1 was good quality, 2 was medium quality and 3 was poor quality. Only photos that received a quality grade of 1 or 2, and no more than two grades of 2 in combination of pitch, arch and roll were used in the further analyses (Christiansen et al., 2018).

Variables

Respiration rate and swim speed

From the focal follow video recording, each respiration by the focal animal was recorded using the open-source software Solomon Coder v17.03.22 (<https://solomon.andraspeter.com/>). The respiration rate of the focal animal was estimated for each flight by dividing the number of respirations by the duration of the focal follow. Focal follows shorter than 5 min in duration were removed from analyses, as shorter follows were found to overestimate respiration rates in right whales (Azizeh et al., 2021) (Fig. S1). The swim speed of the focal animal was estimated from the GPS positional data recorded by the UAV when centred over the focal animal. The positional data were subsampled to 5 s intervals to avoid erratic movements by the UAV. A speed filter of 10 m s⁻¹ was

used to avoid erroneous measurements. The swim speed was then averaged over each video recording (one per flight). Only focal follows which had positional data for more than 70% of the focal follow duration were included in analyses. Animals taking part in mating groups were removed from the analyses, as their sinuous underwater movement could not be accurately captured by the UAV.

Body size and condition

From the aerial photographs, the body length and width (at 5% increments along the body of the whale) were measured, in pixels, using the approach of Christiansen et al. (2016a). Measurements were converted from pixels to metres using the known resolution of the pictures (4608×3456 pixels), the size of the camera sensor (17.3×13 mm), the altitude of the UAV (obtained from the range finder) and the focal length of the camera (25 mm) (for details, see Christiansen et al., 2018). Measurements were taken using a custom-written script in R (<http://www.R-project.org/>; free script available from Christiansen et al., 2016a). For each width measurement, the corresponding height (dorso-ventral distance) was calculated using the known height:width ratio of right whales (Christiansen et al., 2019). The body volume (BV) of each whale was then estimated by modelling the body shape of the whales as a series of infinitesimal ellipses (Christiansen et al., 2019).

The body condition (BC), representing the relative body volume (proportion) of an individual compared with the average (expected) volume of the sample population, was calculated using the formula of Christiansen et al. (2018):

$$BC_i = \frac{BV_{Obs,i} - BV_{Exp,i}}{BV_{Exp,i}}, \quad (1)$$

where $BV_{Obs,i}$ is the observed body volume of whale i , in m³, and $BV_{Exp,i}$ is the expected (or predicted) body volume of whale i , in m³, given by the log–log relationship between body volume and body length, in m, of right whales from the Head of Bight (Christiansen

et al., 2022b; Fig. S2):

$$\log(\text{BV}_{\text{Exp},i}) = -4.115 + 3.016 \times \log(\text{BL}_i). \quad (2)$$

The body mass (BM_{Exp}), in kg, of each whale i was calculated from:

$$\text{BM}_{\text{Exp},i} = \exp(-4.115 + 3.016 \times \log(\text{BL}_i)) \times 805, \quad (3)$$

where 805 is the body density, in kg m^{-3} volume, of a right whale in average body condition ($\text{BC}=0$), based on Christiansen et al. (2022b).

Individual ID and reproductive class

Individual whales were identified using the unique callosity pattern on their heads (Payne et al., 1983), and classified into specific reproductive classes: calves, juveniles, adults, pregnant and lactating females. Calves and lactating females were classified based on their relative size (calves are $<2/3$ the length of their mothers; Christiansen et al., 2018) and close association with each other. Juveniles and NPNL adults were separated based on a body length threshold of 12.0 m (Christiansen et al., 2020c). Adults that were later observed with a dependent calf within the same breeding season were classified as pregnant.

Analyses

Energy expenditure metrics

We estimate two metrics to represent energy expenditure. The first, FMR, was inferred through respiration rate, and reflects the catabolized energy (in J) needed for maintenance and activity over 24 h. The second was TEE, which was inferred through the rate of loss in body condition, and represents the sum of the catabolized (for maintenance and activity) and deposited (for somatic growth, fat deposition and transfer to offspring) energy (in J) over 24 h.

Effects of body size, activity and reproductive class on respiration rate

To quantify the energetic costs of body maintenance, activity and reproduction for right whales, linear mixed effect models (LMMs) were developed in R 4.0.3 (<http://www.R-project.org/>). Respiration rate was used as the response variable and body length, swim speed and reproductive class (NPNL animals versus pregnant/lactating females) were used as fixed effects (explanatory variables) in the model. To account for the curvilinear relationship between respiration rate and body length, both variables were log-transformed. Swim speed was fitted as a quadratic term to account for the curvilinear increase in respiration rate with increased swim speed (Williams et al., 1993; Yazdi et al., 1999). Repeated measurements of the same individuals were accounted for by including animal ID as a random effect in the model. The same model was also developed using body mass instead of body length to represent size. Model selection was done using Akaike's information criterion (AIC). The marginal (R_m^2) and conditional (R_c^2) R^2 of the models were calculated using the 'MuMIn' package to quantify the variance explained by the fixed effects and the variance explained by both the fixed and random effects, respectively (Nakagawa and Schielzeth, 2013). Model validation tests included scatterplots of residual versus fitted values (to test for homogeneity in model residuals) and residual histograms (to test for normality of residuals). We also tested whether calf body length (both absolute and relative) had an effect on the model residuals for the respiration rate of lactating females, which could reflect the increased cost of milk production as the calf grows in body size over the breeding season (Fig. S3). We found no such effect and all models fulfilled the assumptions.

To determine the respiratory cost of transport (COT_{RR}) for right whales, we calculated the number of breaths needed to swim 1 km:

$$\text{COT}_{\text{RR},i} = \frac{\text{RR}_i \times 1000}{\text{SV}_i \times 60}, \quad (4)$$

where RR_i and SV_i are the respiration rate, in breaths min^{-1} , and swim speed (velocity), in m s^{-1} , of whale i , respectively. While surface currents could have influence the measured swim speeds of right whales, the animals were swimming in all possible directions throughout the day (Fig. 1), which means that any bias would have been balanced out.

Inferring field metabolic rate from respiration rate

Using the respiration rate data, assuming a constant tidal volume and oxygen extraction (Folkow and Blix, 1992; Rojano-Doñate et al., 2018; Yazdi et al., 1999), we estimated (inferred) the FMR, in kJ day^{-1} , for right whales from:

$$\text{FMR}_i = \dot{V}_{\text{O}_2} \times 20.1 \times 60 \times 24, \quad (5)$$

where $20.1 \text{ kJ l}^{-1} \text{ O}_2$ is the calorific coefficient of oxygen (Folkow and Blix, 1992) and \dot{V}_{O_2} is the rate of oxygen consumption, in $\text{l O}_2 \text{ min}^{-1}$, given by:

$$\dot{V}_{\text{O}_2} = V_t \times \text{RR}_i \times F_{\text{O}_2} \times E_{\text{O}_2}, \quad (6)$$

where V_t is the tidal volume (the volume of air inspired per breath), in l breath^{-1} , RR is the measured respiration rate, in breaths min^{-1} , F_{O_2} is the fraction of oxygen in atmospheric air, assumed to be 0.2095, and E_{O_2} is the oxygen extraction (the fraction of oxygen extracted in the lungs during a respiratory cycle), assumed to be 0.35 (95% confidence interval, $\text{CI}=0.30\text{--}0.40$; Videsen et al., 2023). The tidal volume V_t was assumed to be 60% (95% $\text{CI}=40\text{--}80\%$) of the vital capacity (V_c , the maximum possible tidal volume), in litres (Folkow and Blix, 1992; Wahrenbrock et al., 1974; Videsen et al., 2023). Following the approach of Videsen et al. (2023), V_c was in turn assumed to be 85% of the total lung capacity (TLC) (Fahlman et al., 2015; Kooyman, 1973; Kooyman et al., 1981; Olsen et al., 1969), where TLC, in litres, was calculated from the allometric relationship for V_c given by Kooyman (1973):

$$\text{TLC} = 0.135 \times \text{BM}_{\text{Exp},i}^{0.92}, \quad (7)$$

where $\text{BM}_{\text{Exp},i}$ represent the body mass of right whale i in average body condition ($\text{BC}=0$) from Eqn 3. Combined, the FMR of a right whale, in kJ day^{-1} , can be estimated from their body mass and respiration rate:

$$\text{FMR}_i = (0.6 \times 0.85 \times (0.135 \times \text{BM}_{\text{Exp},i}^{0.92}) \times \text{RR}_i \times 0.2095 \times 0.35 \times 20.1) \times 60 \times 24. \quad (8)$$

The energetic cost of transport (COT_E), the energy needed to move 1 kg of body mass 1 m, was estimated for different-sized right whales from:

$$\text{COT}_{E,i} = \frac{\text{FMR}_i/24/60/60}{\text{SV}_i \times \text{BM}_i}. \quad (9)$$

The mean FMR per breath, in kJ breath^{-1} , was estimated from:

$$\text{FMR}(\text{breath})_i = \frac{\text{FMR}_i}{\text{RR}_i \times 60 \times 24}. \quad (10)$$

To account for uncertainty in model parameter values, we also calculated FMR based on the upper and lower 95% CI

for E_{O_2} (0.30–0.40) and the assumed percentage of V_t relative to V_c (40–80%) (Videsen et al., 2023).

Intra-seasonal rate of loss in body condition

To determine the metabolically active body region of right whales, the site-specific changes in relative body width within breeding seasons were investigated using linear models (LMs) in R (Christiansen et al., 2016a, 2018, 2021). Separate models were fitted for each width measurement site and for each reproductive class.

To infer the relative energy expenditure of right whales, LMMs were developed in R to investigate the intra-seasonal variation in body condition of different reproductive classes. Body condition was used as the response variable, and day of year (Julian day) and reproductive class (calves, juveniles, adults, pregnant and lactating females) were used as fixed effects in the model. To account for potential annual variations in body condition of whales, we included year and year conditional on reproductive class as covariates. To account for repeated measurements of the same individual over a season, animal ID was included as a random effect in the model. Model selection was carried out using AIC. The same model validation test was performed as for the respiration rate analyses, and all models fulfilled the model assumptions.

To see how our cross-sectional body condition model (based on the entire sample population) captured individual variation in body condition over the breeding season, we also calculated the rate of loss in body condition of individual whales using separate LMs for each animal and then compared this with the population average from the LMM (Fig. S4). Following the recommendation of Christiansen et al. (2018), we restricted our analyses to individuals that had been measured at least four times and for which the duration between the first and last measurement was at least 20 days.

Inferring TEE from body condition loss

Christiansen et al. (2022b) showed that variation in the morphometric body condition of right whales was caused by changes in blubber mass (and consequent volume), while other tissues (muscle, viscera and bone) remained relatively constant in mass with varying body condition. Hence, by knowing the density of blubber, and its energy content, we converted the rate of loss in body condition (ΔBC) of different reproductive classes (Rep.class) of right whales to infer TEE, in kJ day^{-1} :

$$\text{TEE}_{\text{Rep.class}} = \Delta BC_{\text{Rep.class}} \times BV_{\text{Exp,Rep.class}} \times D_{\text{Blubber}} \times E_{\text{Blubber}}, \quad (11)$$

or if we replace $BV_{\text{Exp,Rep.class}}$ with Eqn 2:

$$\text{TEE}_{\text{Rep.class}} = \Delta BC_{\text{Rep.class}} \times \exp(-4.115 + 3.016 \times \log(\text{BL}_{\text{Rep.class}})) \times D_{\text{Blubber}} \times E_{\text{Blubber}}, \quad (12)$$

where $\text{BL}_{\text{Rep.class}}$ is based on the mean body length of the specific reproductive class, D_{Blubber} is the tissue density of blubber, assumed to be 700 kg m^{-3} based on the food density database of the Food and Agriculture Organization of the United Nations (Charrondiere et al., 2012) and E_{Blubber} is the energy content, in kg m^{-3} , of blubber, which is given by its lipid content. Although blubber also contains proteins, capital breeding marine mammals generally catabolize lipids and not protein during periods of fasting (Costa et al., 1986; Crocker et al., 2014; Ortiz et al., 2010). We therefore assumed that only blubber lipids were catabolized by the whales,

and no proteins. Montie et al. (2010) reported blubber lipid concentrations ranging from 54% and 68% for three stranded juvenile and one adult North Atlantic right whale (*Eubalaena glacialis*). Further, the lipid concentration of blubber, and hence its energy content, is known to vary across the body of baleen whales, seasonally and also between species and reproductive classes (Aguilar and Borrell, 1990; Lockyer, 1987; Lockyer et al., 1984, 1985; Vikingsson, 1990; Vikingsson et al., 2013). Therefore, we used three different values of lipid concentration in our calculations: 40%, 60% and 80%. The calorific equivalents of lipids was assumed to be $39,539 \text{ kJ kg}^{-1}$ ($9450 \text{ kcal kg}^{-1}$) wet mass (Brody, 1968; Lockyer et al., 1985). Blubber energy loss was estimated from the rate of BC loss for all reproductive classes, except for calves, which did not fast through the breeding season.

For each reproductive class, the body condition loss per breath, in proportion breath^{-1} , was calculated from:

$$\text{BC}(\text{breath})_{\text{Rep.class}} = \frac{\Delta BC_{\text{Rep.class}}}{\text{RR}_{\text{Rep.class}} \times 60 \times 24}, \quad (13)$$

where $\Delta BC_{\text{Rep.class}}$ is the mean rate of loss in body condition, in proportion day^{-1} , and $\text{RR}_{\text{Rep.class}}$ is the mean respiration rate, in breaths min^{-1} , of the specific reproductive class.

To allow comparison between the calculated FMR of right whales based on respiration rate and the estimated TEE based on body condition loss, we also calculated the mean TEE per breath, in kJ breath^{-1} , from the body condition rate of loss:

$$\text{TEE}(\text{breath})_{\text{Rep.class}} = \frac{\text{TEE}_{\text{Rep.class}}}{\text{RR}_{\text{Rep.class}} \times 60 \times 24}. \quad (14)$$

Again, we used the three different values of lipid concentration (40%, 60% and 80%) and excluded calves from the analyses as they did not fast during the breeding season.

RESULTS

UAV focal follow effort

Behavioral focal follows were conducted on right whales at the Head of Bight over 30 days in 2017 and 22 days in 2019 (Fig. 1). The samples were collected between 1 July and 24 September. A total of 776 focal follows were completed (360 calves, 5 juveniles, 23 adults, 27 pregnant and 361 lactating females) of 185 unique individuals (84 calves, 3 juveniles, 7 adults, 7 pregnant and 84 lactating females) (Table 1). The number of focal follows on each whale ranged from 1 to 14, with a median of 3 follows (Table 1). A total of 168 h of focal follow data were recorded, with a mean duration of 13 min (range: 5–20 min).

UAV aerial photogrammetry effort

Data on right whale body condition were collected at the Head of Bight on 175 days between 2016 and 2019 (Fig. 1). Sampling was conducted between late June and late September, with the exception of 2017, when logistical constraints delayed the starting date until mid-July. A total of 9060 measurements were obtained, and after quality filtering (based on camera focus, body posture and body contour clarity), 5372 measurements (60%) remained from 791 whales (Table 2). The vast majority (94.6%) of measurements were of mothers and calves. Individual whales were measured from 1 to 46 times, across a period of 1 to 93 days (Table 2). The body length of right whales was 3.9–8.8 m (mean \pm s.d. 6.3 ± 0.8 m) for calves, 8.9–12.0 m (10.3 ± 0.9 m) for juveniles, 12.0–14.6 m (13.3 ± 0.8 m) for adults, 12.6–14.8 m (13.7 ± 0.6 m) for pregnant females, and 11.7–16.2 m (14.0 ± 0.6 m) for lactating females.

Table 1. Reproductive class composition of southern right whales sampled at the Head of Bight, South Australia, during UAV behavioural focal follows

Year	Date		Sampling effort		No. of focal follows (no. of individuals)				
	Start	End	Period	Days	Calves	Juveniles	Adults	Pregnant	Lactating
2017	15 Jul.	14 Sep.	61	30	195 (42)	0 (0)	0 (0)	0 (0)	196 (42)
2019	1 Jul.	24 Sep.	85	22	165 (42)	5 (3)	23 (7)	27 (7)	165 (42)
Total	1 Jul.	24 Sep.	85	52	360 (84)	5 (3)	23 (7)	27 (7)	361 (84)

'Period' is the duration (in days) between the first day of sampling and the last day of sampling. 'Days' is the number of days of sampling within that period.

Effects of body size, activity and reproductive class on respiration rate of pregnant and lactating whales

The most parsimonious model for right whale respiration rate included body length, swim speed and the reproductive state as explanatory variables, and animal ID as a random effect (Model 8 in Table 3). We found a significant curvilinear negative relationship between respiration rate and body length ($F_{1,588}=1122.9$, $P<0.001$), with an intercept (\pm s.e.) of 4.709 ± 0.2317 breaths min^{-1} (on a log–log scale) and a rate of decline of -2.257 ± 0.120 breaths min^{-1} (on a log–log scale) per metre increase in body length (Fig. 2A). The corresponding relationship for body mass had an intercept of 6.637 ± 0.333 breaths min^{-1} (on a log–log scale) and a rate of decline of -0.748 ± 0.040 breaths min^{-1} (on a log–log scale) per kilogram increase in body mass (Fig. 2B). We found a significant effect of swim speed on respiration rate ($F_{1,588}=25.8$, $P<0.001$), which increased at a rate of 0.324 ± 0.064 breaths min^{-1} (on a log–log scale) per metre per second increase in swim speed squared (Fig. 2C). Back-transformed to the arithmetic scale, a swim speed of 0.10, 0.25, 0.50 and 1.00 m s^{-1} would increase the respiration rate of a right whale from their stationary respiration rate ($\text{SV}=0$ m s^{-1}) by 0.3%, 2.0%, 8.4% and 38.2%, respectively. Finally, we found a significant difference in respiration rate (intercept) between reproductive classes ($F_{1,588}=13.5$, $P<0.001$), with the respiration rate of pregnant/lactating females being on average 0.363 ± 0.099 breaths min^{-1} (on a log–log scale) higher than that of the other reproductive classes (Fig. 2C). There was no difference in respiration rate between pregnant and lactating females, which were therefore combined. The fixed effects of the full model explained 80.2% (R_m^2) of the variance in the data, while the fixed and random effects together explained 90.2% (R_c^2) of the variance. From the most parsimonious LMM (Model 8 in Table 3), the equations to estimate the respiration rate (RR), in breaths min^{-1} , of right whales for NPNL animals (calves, juveniles and adults) as a function of body length (BL_i) or body mass (BM_i) were:

$$\text{RR}_{\text{NPNL},i} = \exp(4.709 - 2.257 \times \log(\text{BL}_i) + 0.324 \times \text{SV}_i^2), \quad (15)$$

$$\text{RR}_{\text{NPNL},i} = \exp(6.637 - 0.748 \times \log(\text{BM}_i) + 0.324 \times \text{SV}_i^2). \quad (16)$$

The equivalent formulas for pregnant and lactating females were:

$$\text{RR}_{\text{PL},i} = \exp(4.709 - 2.257 \times \log(\text{BL}_i) + 0.324 \times \text{SV}_i^2 + 0.363), \quad (17)$$

$$\text{RR}_{\text{PL},i} = \exp(6.637 - 0.748 \times \log(\text{BM}_i) + 0.324 \times \text{SV}_i^2 + 0.363). \quad (18)$$

COT_{RR} for right whales varied from 2.6 to 237 breaths km^{-1} across the observed range of swim speeds (0.12–1.11 m s^{-1}) (Fig. 2D). COT_{RR} declined rapidly with swim speed to its lowest estimate at 1.11 m s^{-1} (4.0 km h^{-1}) (Fig. 2D). Back-transformed to the arithmetic scale, the optimal swim speed corresponded to an increase from the stationary respiration rate ($\text{SV}=0$ m s^{-1}) of 49.0%.

Inferred FMR from respiration rate

The mass-specific FMR of right whales followed the same pattern as respiration rate, and declined with increased body length (Fig. 2A) and body mass (Fig. 2B), and increased with swim speed (Fig. 2C). The FMR of a right whale, in kJ day^{-1} , could be estimated from:

$$\text{FMR}_{\text{NPNL},i} = (0.6 \times 0.85 \times (0.135 \times \text{BM}_i^{0.92}) \times \text{RR}_i \times 0.2095 \times 0.35 \times 20.1) \times 60 \times 24, \quad (19)$$

which combined with Eqns 3 and 15 for NPNL whales gives:

$$\begin{aligned} \text{FMR}_{\text{NPNL},i} = & (0.6 \times 0.85 \times (0.135 \times (\exp(-4.115 + 3.016 \\ & \times \log(\text{BL}_i)) \times 805)^{0.92}) \times \exp(4.709 - 2.257 \\ & \times \log(\text{BL}_i) + 0.324 \\ & \times \text{SV}_i^2) \times 0.2095 \times 0.35 \times 20.1) \\ & \times 60 \times 24. \end{aligned} \quad (20)$$

Table 2. Reproductive class composition of southern right whales sampled at the Head of Bight, South Australia, by UAV aerial photogrammetry

Year	Date		Sampling effort		No. of BC measurements (no. of individuals)				
	Start	End	Period	Days	Calves	Juveniles	Adults	Pregnant	Lactating
2016	24 Jun.	25 Sep.	93	49	1090 (89)	18 (14)	39 (20)	3 (3)	865 (84)
2017	13 Jul.	25 Sep.	74	40	405 (87)	6 (5)	22 (17)	1 (1)	410 (85)
2018	23 Jun.	24 Sep.	93	41	410 (88)	44 (20)	53 (30)	31 (11)	537 (90)
2019	28 Jun.	24 Sep.	88	45	662 (67)	28 (14)	24 (14)	19 (11)	705 (67)
Total	24 Jun.	25 Sep.	93	175	2567 (331)	96 (53)	138 (81)	54 (26)	2517 (326)

$n=5372$ measured whales (791 individuals). BC, body condition.

Table 3. Results of the linear mixed effect model selection for southern right whale respiration rate based on minimization of Akaike's information criterion

Model	Fixed effects	Random effects	k	n	Groups	R_m^2	R_c^2	AIC	Δ AIC
1	$\log(\text{RR}) \sim 1$ (null)	$\sim \text{Animal.ID}$	1	776	185	0.000	0.885	924.1	421.2
2	$\log(\text{RR}) \sim \log(\text{BL})$	$\sim \text{Animal.ID}$	2	776	185	0.794	0.897	530.9	28.0
3	$\log(\text{RR}) \sim \text{SV}^2$	$\sim \text{Animal.ID}$	2	776	185	0.010	0.894	892.3	389.4
4	$\log(\text{RR}) \sim \text{Rep.class}$	$\sim \text{Animal.ID}$	2	776	185	0.544	0.883	750.5	247.6
5	$\log(\text{RR}) \sim \log(\text{BL}) + \text{SV}^2$	$\sim \text{Animal.ID}$	3	776	185	0.796	0.902	511.3	8.4
6	$\log(\text{RR}) \sim \log(\text{BL}) + \text{Rep.class}$	$\sim \text{Animal.ID}$	3	776	185	0.801	0.897	521.8	18.9
7	$\log(\text{RR}) \sim \text{SV}^2 + \text{Rep.class}$	$\sim \text{Animal.ID}$	3	776	185	0.539	0.887	728.5	225.6
8	$\log(\text{RR}) \sim \log(\text{BL}) + \text{SV}^2 + \text{Rep.class}$	$\sim \text{Animal.ID}$	4	776	185	0.802	0.902	502.9	0.0

RR, respiration rate; BL, body length; SV, swim speed (velocity); Rep.class, reproductive class [non-pregnant non-lactating (NPNL) animals versus pregnant/lactating females]; Animal.ID, number of individual whales identified (Groups); k , number of model parameters; n , sample size; R_m^2 , marginal R^2 (variance explained by fixed effects); R_c^2 , conditional R^2 (variance explained by fixed and random effects); AIC, Akaike's information criterion. The most parsimonious model is in bold.

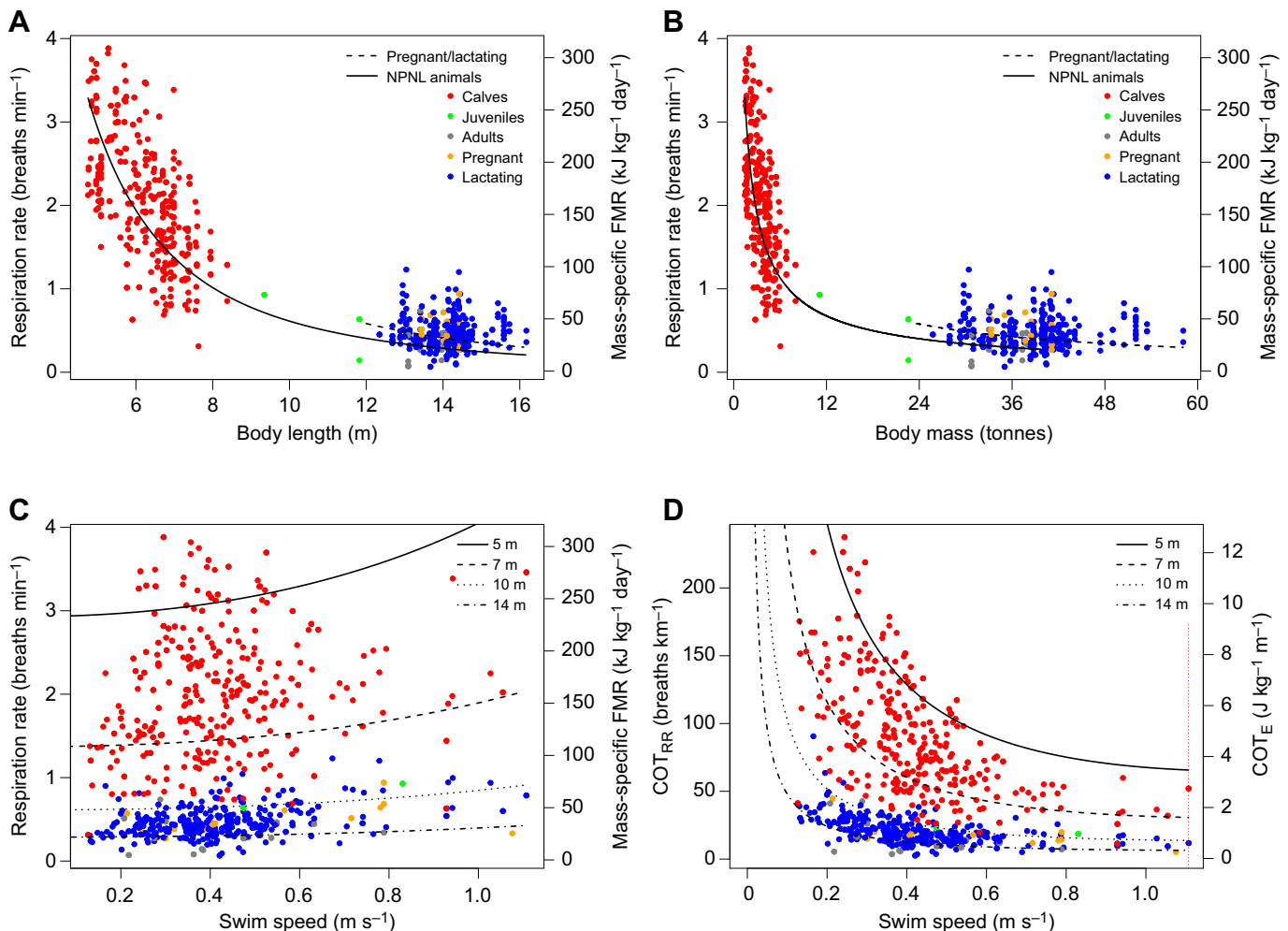


Fig. 2. Effects of body size and activity on respiration rate of southern right whales of different reproductive classes. (A,B) Partial effect plots of southern right whale respiration rate and mass-specific field metabolic rate (FMR) as a function of (A) body length and (B) body mass. The solid and dashed lines represent the predicted values for non-pregnant/non-lactating (NPNL) animals and pregnant/lactating females, respectively. The swim speed was fixed at 0 m s⁻¹ (stationary). The colour of the data points indicates the different reproductive classes (see key) of the raw data. (C) Partial effect plot of respiration rate and mass-specific FMR as a function of swim speed. (D) Respiratory and energetic cost of transport (COT) for right whales as a function of swim speed. The fitted lines in C and D represent the predicted values of NPNL animals of different body lengths (see key). The dotted red vertical line indicates the minimum measured COT at 1.1 m s⁻¹ (4.0 km h⁻¹) swim speed. $n=360$ calves, $n=5$ juveniles, $n=23$ adults, $n=27$ pregnant and $n=361$ lactating females.

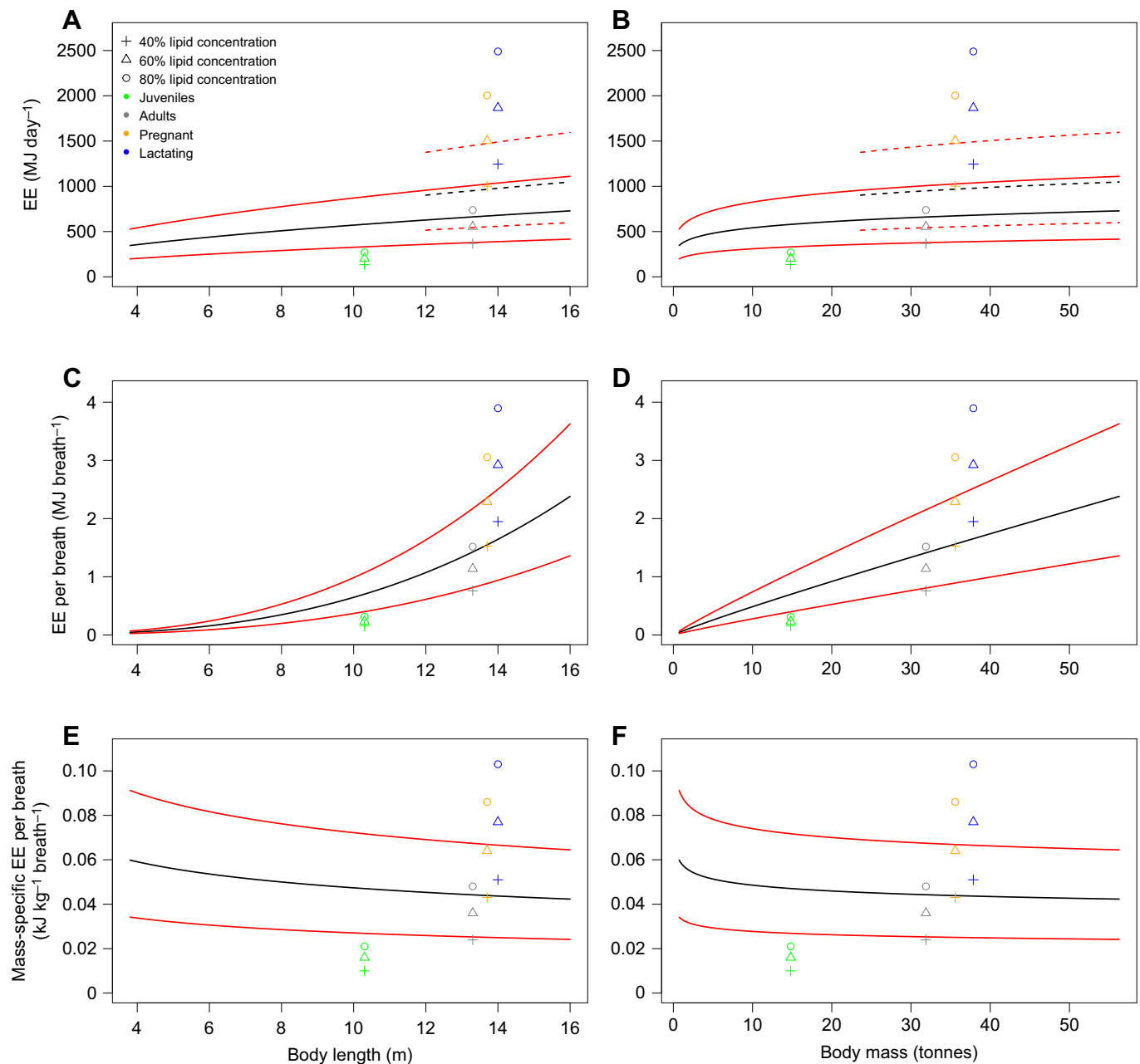


Fig. 3. Energy expenditure according to respiration rate and body condition loss. (A,B) Estimated energy expenditure (EE), (C,D) energy expenditure per breath, and (E,F) mass-specific energy expenditure per breath of southern right whales based on respiration rate (FMR; lines) and body condition loss (total energy expenditure, TEE; symbols) as a function of body length (left) and body mass (right). The solid and dashed black lines represent the mean FMR estimates for NPNL and pregnant/lactating whales, respectively. The red lines represent the 95% confidence intervals (CI). TEE estimates, based on body condition loss, are presented for each reproductive class (see key) based on different blubber lipid concentrations (40–80%, see key).

The equivalent formulas for pregnant and lactating females were:

$$\begin{aligned} \text{FMR}_{\text{PL},i} = & (0.6 \times 0.85 \times (0.135 \times (\exp(-4.115 + 3.016 \\ & \times \log(\text{BL}_i)) \times 805)^{0.92}) \times \exp(4.709 - 2.257 \\ & \times \log(\text{BL}_i) + 0.324 \times \text{SV}_i^2 + 0.363) \\ & \times 0.2095 \times 0.35 \times 20.1) \times 60 \times 24. \end{aligned} \quad (21)$$

The FMR of right whales increased curvilinearly with body length from 346.2 MJ day⁻¹ at 3.8 m body length (737 kg body mass) to 728.6 MJ day⁻¹ at 16.0 m body length (56,288 kg body mass)

(Fig. 3A,B). COT_E declined with increased swim speed to its minimum estimate at 1.1 m s⁻¹ (4.0 km h⁻¹) (Fig. 2D).

The mean FMR per breath increased curvilinearly with body length from 0.044 MJ breath⁻¹ at 3.8 m body length to 2.381 MJ breath⁻¹ at 16.0 m body length (Fig. 3C). The positive relationship between FMR per breath and body mass was close to linear, with a slope of 42.1 kJ breath⁻¹ per tonne increase in body mass (Fig. 3D). The corresponding mass-specific FMR per breath was fairly constant across animals of different sizes (both length and mass), and only decreased slightly from 0.060 kJ kg⁻¹ breath⁻¹ at 3.8 m body length (737 kg body mass) to 0.042 kJ kg⁻¹ breath⁻¹ at 16.0 m body length (56,288 kg body

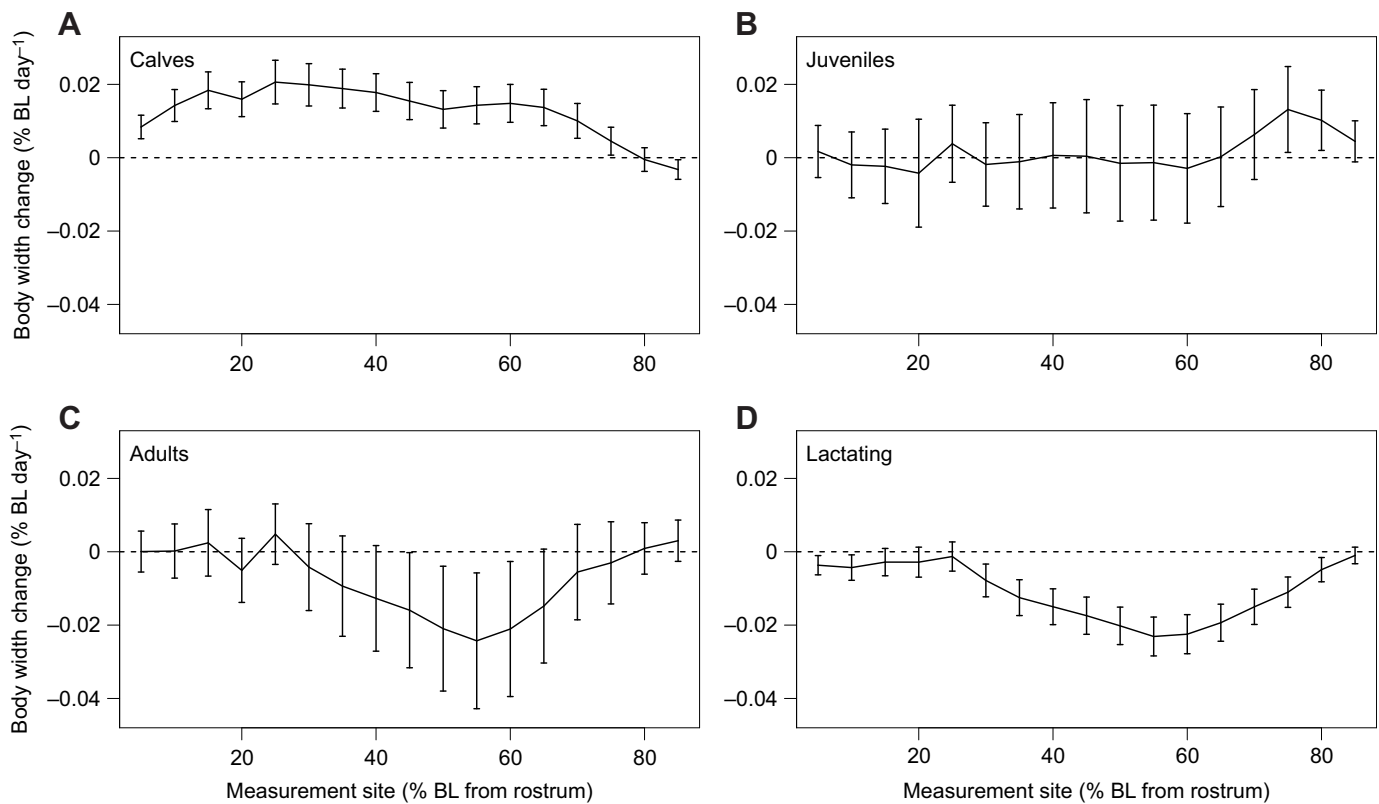


Fig. 4. Rate of change of body width of southern right whales of different reproductive classes. Relative change in body width (W , as a percentage of body length, BL) at different measurement sites of (A) calves ($n=331$), (B) juveniles ($n=53$), (C) adults ($n=81$) and (D) lactating females ($n=326$). The solid black line represents the day effect (i.e. slope parameter, β), based on the linear model: $W/BL = \alpha + \beta \times \text{day}$. Error bars represent the lower and upper 95% CI. The dashed lines represent the level where relative body width remains constant ($\beta=0$) throughout the breeding season.

mass) (Fig. 3E,F), which equalled a 29.3% decline in mass-specific cost per breath.

Intra-seasonal rate of loss in body condition

The body morphometric data showed that the body of right whales was widest at approximately 30% BL from the rostrum for all five reproductive classes (Fig. S5). The intra-seasonal change in body width varied between measurement sites and reproductive classes (Fig. 4). Calves increased in relative body width all across the body, from 5% to 75% BL from the rostrum, with the most significant increase at the mid-region of the body, from 25% to 60% BL from the rostrum (Fig. 4A). Juveniles showed no visible decline in body width across the body throughout the breeding season, whereas adults decreased between 40% and 70% BL from the rostrum (Fig. 4B,C). Lactating females decreased significantly in body width across most of the body, from 30% to 80% BL from the

rostrum, with the most significant thinning occurring between 40% and 75% BL from the rostrum (Fig. 4D).

The LMM that best described the observed variation in body condition of right whales included reproductive class ($F_{4,4572}=77.1$, $P<0.001$) and day of year conditional (interaction term) on reproductive class ($F_{5,4572}=638.7$, $P<0.001$) as covariates (Model 6 in Table 4). The fixed effects of the model explained 23.7% (R_m^2) of the variance in body condition, while the fixed and random effects together explained 81.5% (R_c^2) of the variance, suggesting a large individual effect. Among the non-dependent reproductive classes, adults had the lowest body condition at the beginning (24 June) of the breeding season, at $2.0 \pm 1.7\%$ (\pm s.e.), and this decreased at a rate of $-0.084 \pm 0.0365\%$ per day (Fig. 5). Juveniles started the breeding season in slightly better body condition, at $5.6 \pm 2.4\%$, and this decreased at a relatively slower rate of $-0.066 \pm 0.0458\%$ per day (Fig. 5). Pregnant and lactating females

Table 4. Results of the linear mixed effect model selection for southern right whale body condition based on minimization of Akaike's information criterion

Model	Fixed effects	Random effects	k	n	Groups	R_m^2	R_c^2	AIC	Δ AIC
1	BC~1 (null)	~Animal.ID	1	5375	791	0.000	0.600	-12,297.3	2463.5
2	BC~Day	~Animal.ID	2	5375	791	0.011	0.611	-12,353.8	2407.0
3	BC~Year	~Animal.ID	4	5375	791	0.018	0.599	-12,288.9	2471.9
4	BC~Rep.class	~Animal.ID	5	5375	791	0.024	0.618	-12,437.7	2323.1
5	BC~Rep.class+Day	~Animal.ID	6	5375	791	0.029	0.624	-12,458.9	2301.9
6	BC~Rep.class*Day	~Animal.ID	10	5375	791	0.238	0.813	-14,760.8	0.0

BC, body condition; Rep.class, reproductive class (calf, juvenile, adult, pregnant, lactating); Animal.ID, number of individual whales (Groups); k , number of model parameters; n , sample size; R_m^2 , marginal R^2 (variance explained by fixed effects); R_c^2 , conditional R^2 (variance explained by fixed and random effects). The most parsimonious model is in bold.

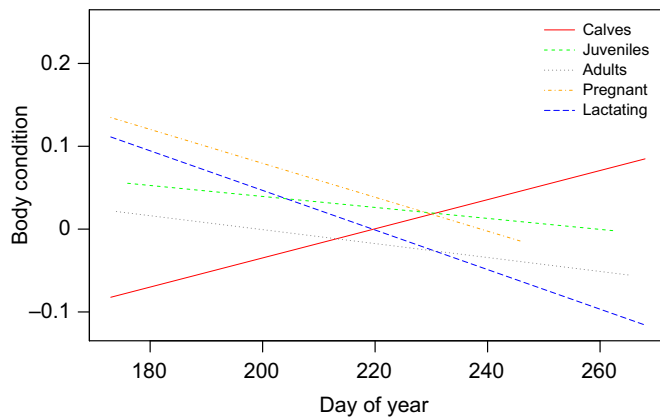


Fig. 5. Intra-seasonal change in body condition of different reproductive classes of southern right whales at the Head of Bight, South Australia. The solid and dashed lines represent the fitted values of the most parsimonious model (Model 6 in Table 4). $n=5372$ measurements (see Table 2 for sample composition).

had the highest body condition at the beginning of the breeding season, at $13.1 \pm 1.1\%$ and $10.6 \pm 0.6\%$, respectively. The rate of loss in body condition was similar between the two reproductive classes, at $-0.205 \pm 0.0459\%$ and $-0.239 \pm 0.0053\%$ per day, respectively (Fig. 5). Although calves were born in relatively low body condition at the beginning of the breeding season, at $-7.9 \pm 0.6\%$, they increased in condition at a rate of $0.176 \pm 0.0052\%$ per day as they grew in overall body size (Fig. 5). At the end of the breeding season (25 September), calves had a mean body condition of $8.5 \pm 0.5\%$, whereas juveniles, adults and lactating females (there are no pregnant females at the end of the breeding season) were in increasingly poorer condition, at $-0.6 \pm 2.6\%$, $-5.8 \pm 2.3\%$ and $-11.6 \pm 0.6\%$, respectively (Fig. 5). The equations to describe the intra-seasonal body condition (BC; as a proportion) of different reproductive classes of whales were:

$$BC_{\text{Calves}} = -0.3865 + 0.00176 \times \text{Day}, \quad (22)$$

$$BC_{\text{Juveniles}} = 0.1720 - 0.00066 \times \text{Day}, \quad (23)$$

$$BC_{\text{Adults}} = 0.1676 - 0.00084 \times \text{Day}, \quad (24)$$

$$BC_{\text{Pregnant}} = 0.4889 - 0.00205 \times \text{Day}, \quad (25)$$

$$BC_{\text{Lactating}} = 0.5247 - 0.00239 \times \text{Day}. \quad (26)$$

The rate of loss in individual body condition was successfully calculated for 161 lactating females that fulfilled the sample size criteria (minimum of 4 samples over a minimum of 20 days) (Fig. S4). The mean rate of loss in body condition of individual lactating females was $0.257 \pm 0.089\% \text{ day}^{-1}$ (mean \pm s.d.) (Fig. S4), which was similar to the $0.239\% \text{ day}^{-1}$ estimated by the cross-sectional LMM (Fig. 5). Unfortunately, we did not have enough data to calculate the corresponding individual rates of loss in body condition of the other reproductive classes.

Inferred TEE from body condition loss

The calculated body condition energy loss (TEE) of different reproductive classes of right whales was $135.1\text{--}270.2 \text{ MJ day}^{-1}$ for juveniles, $368.9\text{--}737.9 \text{ MJ day}^{-1}$ for adults, $1001.8\text{--}2003.6 \text{ MJ day}^{-1}$ for pregnant females and $1244.8\text{--}2489.6 \text{ MJ day}^{-1}$ for lactating females, depending on the assumed blubber energy content (Table 5, Fig. 3A,B). The body condition loss per breath was $7.6 \times 10^{-7} \text{ prop. breath}^{-1}$ for juveniles, $17.3 \times 10^{-7} \text{ prop. breath}^{-1}$ for adults, $31.2 \times 10^{-7} \text{ prop. breath}^{-1}$ for pregnant females and

$37.4 \times 10^{-7} \text{ prop. breath}^{-1}$ for lactating females (Table 5). The TEE per breath was $0.155\text{--}0.310 \text{ MJ breath}^{-1}$ for juveniles, $0.759\text{--}1.517 \text{ MJ breath}^{-1}$ for adults, $1.526\text{--}3.052 \text{ MJ breath}^{-1}$ for pregnant females and $1.948\text{--}3.895 \text{ MJ breath}^{-1}$ for lactating females, depending on the assumed blubber energy content (Table 5, Fig. 3C,D). The corresponding mass-specific TEE per breath was $0.010\text{--}0.021 \text{ kJ kg}^{-1} \text{ breath}^{-1}$ for juveniles, $0.024\text{--}0.048 \text{ kJ kg}^{-1} \text{ breath}^{-1}$ for adults, $0.043\text{--}0.086 \text{ kJ kg}^{-1} \text{ breath}^{-1}$ for pregnant females and $0.051\text{--}0.103 \text{ kJ kg}^{-1} \text{ breath}^{-1}$ for lactating females, depending on the assumed blubber energy content (Table 5, Fig. 3E,F).

DISCUSSION

By utilizing novel UAV focal follow (Nielsen et al., 2019a; Sprogis et al., 2020a) and aerial photogrammetry (Christiansen et al., 2016a, 2018) methods, this study quantifies the effect of body size, activity level and reproductive state on the energy expenditure (FMR and TEE) of a capital breeding baleen whale, the southern right whale. We show that right whale mass-specific FMR, inferred from respiration rate, decreased exponentially with body size, as expected based on allometric scaling (Kleiber, 1932). The respiration rate and FMR increased curvilinearly with swim speed, probably as a result of increased drag and activity level (Williams et al., 1993; Yazdi et al., 1999). Respiration rate and FMR were also overall higher for pregnant and lactating females, probably due to the added costs of fetus maintenance (heat of gestation) and milk production, respectively (Christiansen et al., 2018; Lockyer, 1981a). Our two modelling approaches (FMR based on respiration rate versus TEE based on body condition loss) yielded similar estimates of energy expenditure for adult whales. For pregnant/lactating females, FMR estimates were lower than the calculated TEE. This discrepancy is probably due to the significant amount of energy that is being transferred from the mother to the foetus (for pregnant females) and the calf (in the form of milk for lactating females), which is not reflected in the mother's respiration rate.

In accordance with hypothesis I, the respiration rate and mass-specific FMR of right whales decreased exponentially with increased body size. Although this relationship has been reported across a large number of terrestrial and marine organisms (Calder, 1984; Kleiber, 1947; Peters, 1983; Schmidt-Nielsen, 1984), this is the first study to empirically demonstrate this for a baleen whale species. A decline in calf respiration rate as a function of body length (and mass) was reported for right whales by Nielsen et al. (2019a) and for humpback whales (*Megaptera novaeangliae*) by Ejrnæs and Sprogis (2021). However, as both studies divided calves and mothers into separate analyses, they were unable to detect the same curvilinear relationship as reported in this study. By accounting for the activity state of the animal (by setting swim speed to zero in Eqns 20 and 21), our estimates of respiration rates represent the cost of maintenance for right whales. Compared with measured FMR for marine mammals (Rimbach et al., 2021), our estimate for adult NPNL whales, based on respiration rate, is considerably lower than what would be expected based on allometric scaling (Fig. S6). Instead, our estimate is closer to what would be expected for terrestrial mammals if the allometric equation from Rimbach et al. (2021) is extrapolated (Fig. S6). If our estimate is correct, it would mean that right whales do not exhibit the same elevated FMR as smaller marine mammals (Acquarone et al., 2006; Maresh et al., 2014; Nagy et al., 1999; Rojano-Doñate et al., 2018), which is believed to be a reflection of the high cost of endothermy in marine environments. Baleen whales might not exhibit this cost because of a reduction in heat loss caused by their larger body size

Table 5. Estimated field metabolic rate (FMR) and total energy expenditure (TEE) of different reproductive classes of southern right whales based on measured respiration rate and intra-seasonal rate of loss in body condition, respectively

Reproductive class	Juveniles	Adults	Pregnant	Lactating
Mean body length (m)	10.3	13.3	13.7	14.0
Mean body volume (m ³)	18.4	39.6	44.2	47.0
Mean body mass (kg)	14,818	31,886	35,581	37,872
Stationary respiration rate (breaths min ⁻¹)	0.577	0.325	0.431	0.411
Mean swim speed (m s ⁻¹)	0.389	0.342	0.420	0.487
Active respiration rate (breaths min ⁻¹)	0.606	0.338	0.456	0.444
Mean FMR (MJ day ⁻¹)	609.2	687.5	1023.2	1055.3
Lower 95% CI FMR (MJ day ⁻¹)	348.0	392.9	584.7	603.0
Upper 95% CI FMR (MJ day ⁻¹)	928.0	1047.7	1559.2	1608.1
Mean FMR per-breath (MJ breath ⁻¹)	0.70	1.41	1.56	1.65
Mean body condition loss (prop. day ⁻¹)	0.00066	0.00084	0.00205	0.00239
Body condition loss per breath (prop. breath ⁻¹)	7.6×10 ⁻⁷	17.3×10 ⁻⁷	31.2×10 ^{-7*}	37.4×10 ^{-7*}
TEE (MJ day ⁻¹)				
40% blubber lipid concentration	135.1	368.9	1001.8	1244.8
60% blubber lipid concentration	202.6	553.4	1502.7	1867.2
80% blubber lipid concentration	270.2	737.9	2003.6	2489.6
Mass-specific TEE (kJ kg ⁻¹ day ⁻¹)				
40% blubber lipid concentration	9.1	11.6	28.2	32.9
60% blubber lipid concentration	13.7	17.4	42.2	49.3
80% blubber lipid concentration	18.2	23.1	56.3	65.7
TEE per breath (MJ breath ⁻¹)				
40% blubber lipid concentration	0.155	0.759	1.526	1.948
60% blubber lipid concentration	0.232	1.138	2.289	2.922
80% blubber lipid concentration	0.310	1.517	3.052	3.895
Mass-specific TEE per-breath (kJ kg ⁻¹ breath ⁻¹)				
40% blubber lipid concentration	0.010	0.024	0.043	0.051
60% blubber lipid concentration	0.016	0.036	0.064	0.077
80% blubber lipid concentration	0.021	0.048	0.086	0.103

Calves were excluded as they are feeding (nursing) throughout the breeding season. *The estimated TEE for pregnant and lactating females also includes the energy transfer between the mother and the offspring; as this energy is not metabolized by the mother, it is not reflected in her FMR, and hence the calculated breath-specific body condition loss is overestimated.

(lower surface area to volume ratio) and thicker insulative blubber layer, especially in the Balaenidae family (George, 2009; Marón et al., 2021; Miller et al., 2012). It is also possible that right whales experience hypometabolic rates, as has been proposed for the closely related bowhead whale (*Balaena mysticetus*) based on its low core body temperature (George et al., 2021). Alternatively, the discrepancy between our estimate of FMR and that measured for smaller marine mammals (Rimbach et al., 2021) could simply be caused by inherent issues with our modelling approach and/or the assumptions used in our bioenergetic models. Until direct measurements are possible for baleen whales, it is difficult to know whether this discrepancy is methodological or physiological, or both.

While the respiration rate model predicted the mass-specific FMR of juveniles to be higher than that of adults, the TEE estimates based on body condition loss were higher for adults than for juveniles. This difference was also evident in the site-specific changes in body width, where juveniles showed no visible decline across the body, whereas adults decreased in body width between 40% and 70% BL from the rostrum. The same pattern has also been reported for humpback whales (Christiansen et al., 2016a) on their breeding grounds. However, when quantifying the absolute loss in body condition over the breeding season, Christiansen et al. (2020a) found that juvenile humpback whales on migration (from the same population as individuals on the breeding ground in Christiansen et al., 2016a) lost significantly more body condition than adults over the breeding season. The discrepancy between the two studies could be due to differences in the migratory timing among age classes and reproductive states. While Christiansen et al. (2020a) measured humpback whales at the southern end of their migratory route in

Western Australia at the start (June) and end (October) of the breeding season, Christiansen et al. (2016a) measured whales further north on their breeding ground during mid-season, which might have represented animals at different stages in their migratory cycle, and hence in varying body condition. The latter situation is likely to be the same for the sampled juvenile and adult right whales in this study. The mean residency time of juvenile and adult right whales at the Head of Bight is considerably lower (14.7 days) than that of lactating females (40 days) (Charlton, 2017). This is visible in the composition of the sampled whales, which includes few repeated samples of juveniles and adults than for lactating females and calves (Table 2). As a consequence of this, most of the juvenile and adult data points in the body condition model were from different individuals, which might have arrived on the breeding grounds at different times and in different body conditions. This variation in migratory timing could have masked the true decline in body condition of juveniles and adults over the study period (in contrast to lactating females), and could explain the mismatch in estimated FMR from the respiration rate data and the TEE based on the body condition data. Alternatively, the lower apparent loss in morphological body condition of juveniles could be due to a higher blubber lipid concentration in juveniles than in adults. However, such a high relative blubber lipid concentration in juveniles compared with adults is not supported by blubber biochemical analyses from fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*) and minke whales (*Balaenoptera acutorostrata*) (Lockyer, 1987; Vikingsson, 1990; Vikingsson et al., 2013).

In alignment with hypothesis II, the respiration rate and FMR of right whales increased with swim speed, as has been reported for

minke whales (Christiansen et al., 2014a) and gray whales (*Eschrichtius robustus*; Sumich, 1983). At lower swim speeds ($<0.5 \text{ m s}^{-1}$), the respiration rate of right whales remained fairly constant; however, as water drag increased with increasing swim speed (Schmidt-Nielsen, 1997; van der Hoop et al., 2017), the respiration rate of right whales increased curvilinearly. This is in agreement with studies of captive bottlenose dolphins (*Tursiops truncatus*) and migratory gray whales, where both power input and respiration rate increased similarly (Williams et al., 1993; Yazdi et al., 1999). Right whale calves also increase their respiration rate and FMR with an increase in swim speed, which is largely dependent on their mother's swim speed (Nielsen et al., 2019a). The estimated COT decreased with swim speed, similar to what has been recorded for bottlenose dolphins (Yazdi et al., 1999), killer whales (*Orcinus orca*; Williams and Noren, 2009), gray whales (Sumich, 1983) and minke whales (Christiansen et al., 2014a). The measured swim speeds were overall low ($0.12\text{--}1.11 \text{ m s}^{-1}$), and below the range of swim speeds reported for southward migrating right whales ($1.22\text{--}1.81 \text{ m s}^{-1}$) that were satellite tagged off South Africa (Mate et al., 2011). This is probably a result of the data being collected on a nursing ground and not on a migratory route. At these speeds, the added energetic cost of swimming equalled 4.7–49.0% of FMR when stationary ($SV=0 \text{ m s}^{-1}$). The mean swim speeds of the different reproductive classes were even lower ($0.3\text{--}0.5 \text{ m s}^{-1}$), resulting in an added energetic cost of swimming of only 3.0–8.4% of FMR when stationary ($SV=0 \text{ m s}^{-1}$).

In agreement with hypothesis III, the respiration rate and FMR of pregnant and lactating females were overall higher than those of NPNL adults. This difference was even more pronounced when looking at the TEE and rate of body condition loss of pregnant and lactating females, which was 2.4 and 2.8 times higher than that of NPNL adults, respectively. The site-specific body width change showed that lactating females lost body condition across the full range of their metabolically active body region (30–80% BL from rostrum). The most significant decline occurred between 40% and 75%BL from the rostrum, which is consistent with the findings of Christiansen et al. (2018) for southern right whales and Miller et al. (2012) for North Atlantic right whales. Gestation and lactation are considered the most expensive phases in the life cycle of mammals (Gittleman and Thompson, 1988; Oftedal, 1985), and the same holds true for cetaceans (Christiansen et al., 2018, 2022a; Lockyer, 1981a). For right whales, Christiansen et al. (2018) found that the rate of loss in body condition of lactating females was constant (at $0.126 \text{ m}^3 \text{ day}^{-1}$ in body volume) through the first 4 months of lactation. The TEE of lactating females comprises the cost of maternal maintenance and activity, as well as the cost of milk production and energy transfer to the calf (Lockyer, 1981a, 2007; Villegas-Amtmann et al., 2015). The higher respiration rate (intercept) and FMR of lactating females compared with NPNL adults could partly be due to the added cost of milk production. However, milk production has been shown to not increase FMR significantly in marine mammals, as mobilization of body fat does not require *de novo* synthesis of lipids (Costa and Trillmich, 1988; Costa et al., 1986; Fedak and Anderson, 1982). Instead, the respiration rate and FMR of lactating females may be higher as a result of the energetic costs associated with infant carrying behaviour (i.e. echelon swimming and infant position), which is known to decrease locomotor performance and increase locomotor effort in cetaceans (Noren, 2008; Williams and Noren, 2009). The transferred energy to the calf, which was reflected in the high body condition loss and estimated TEE of lactating females, should be roughly equivalent to the energy requirements of the calf, which

comprise calf maintenance, activity and somatic growth (including body fattening). As the calf grows in size through the breeding season, at a mean rate of 3.2 cm day^{-1} in body length and $0.081 \text{ m}^3 \text{ day}^{-1}$ in body volume (Christiansen et al., 2018), its FMR should increase (and its mass-specific FMR decrease), which means that the transferred energy from the mother should increase at a similar rate. However, this is not reflected in the rate of loss in body condition of right whale females, which remains constant throughout the breeding season (Christiansen et al., 2018). A female could potentially maintain a constant rate of body condition loss if she reduces her own energy expenditure, by lowering her activity level. Nielsen et al. (2019a) found support for this, by showing that the respiration rate, and hence FMR, of female right whales decreased over the breeding season as their calves grew in body length. In addition to this, there might not be a linear relationship between body volume loss and lipid catabolism in right whales.

The similarly elevated respiration rate and FMR in pregnant females to that of lactating females was surprising, as the cost of lactation is overall higher than that of gestation in marine mammals (Costa et al., 1986; Fedak and Anderson, 1982; Williams et al., 2007). Pregnant females allocate additional energy to cover the costs of fetal growth (including the placenta) and maintenance (heat of gestation) (Lockyer, 1981b, 2007; Villegas-Amtmann et al., 2015), which increases exponentially through gestation (Christiansen et al., 2022a). For right whales, 95% of the total cost of gestation is incurred during the third trimester (Christiansen et al., 2022a). With the pregnant females in this study representing late-pregnant females (e.g. most of them gave birth within a week or two of being sampled), the cost of gestation for these females was at or near its maximum, which can explain their elevated respiration rate and FMR resulting from the fetus maintenance cost (heat of gestation). In addition, it is well documented that hormonal changes (i.e. increased progesterone levels) during pregnancy can induce respiratory changes in a variety of mammals (Behan et al., 2003; Keith et al., 1982). Finally, fluid dynamics modelling shows that drag increases by 3–4% in pregnant right whales, which could increase locomotor costs (Nousek McGregor, 2010). Immediately after giving birth, right whale females lose about 7.3 percentage points of their body condition as the newborn calf leaves their body (Christiansen et al., 2022a). This is visible in the lower intercept of the body condition slope of pregnant females compared with lactating females (Fig. 5). The rate of decline in body condition of lactating females was slightly higher than for pregnant females, suggesting a higher TEE during early lactation compared with late pregnancy. The difference was small, however, which is probably why no difference in respiration rate and FMR was detected between the two reproductive classes, although hormonal changes might also be contributing to this.

Though this study presents some clear physiological patterns for right whales, there are some inconsistencies and limitations that need to be highlighted. Our estimates of FMR from respiration rates are based on the assumption that the tidal volume and oxygen extraction are constant for right whales. This is a clear simplification, as Roos et al. (2016) showed that there is significant variation in the oxygen uptake between breaths in cetaceans. While this variation in oxygen uptake is likely to have contributed to the large observed variation in right whale respiration rates in this study, the variation is likely to be similar across body sizes for NPNL whales. For pregnant females, however, elevated progesterone levels could be contributing to their elevated respiration rates, as reported in other mammals (Behan et al., 2003; Keith et al., 1982). It is worth adding that the rate of loss of

body condition already incorporates the daily activity level (i.e. swim speed) of the whales, while the FMR estimates from respiration rate require the swim speed to be estimated and added to the calculation (Eqns 20 and 21). The mean swim speed estimates used to calculate the active FMR of different reproductive classes in this study do not account for the potential effects of time of day, day of year and body length on activity level. Further, Nielsen et al. (2019a) found that the swim speed of lactating females decreased as their calves grew in body length (and mass) through the breeding season. Further, with juveniles and adults spending little time in the Head of Bight study area, their estimated swim speeds might not be representative of their activity level over the course of the breeding season, which includes mating behaviour (for adults) and movement between different coastal aggregation areas (Mate et al., 2011; Watson et al., 2021; Zerbini et al., 2018). Also, our swim speed data were restricted to daylight hours only, and hence did not account for potential diel patterns in activity level. By equipping right whales with multi-sensor tags (Johnson and Tyack, 2003) over a 24 h period, this data gap could be filled.

Management implications

With baleen whales playing important ecosystem roles (Roman et al., 2014), understanding their energy expenditure can provide valuable information about their prey requirements (Laidre et al., 2007; Sigurjónsson and Vikingsson, 1997), and vulnerability to future changes in prey availability due to climate change (Tulloch et al., 2019). We estimated the mean TEE (assuming a blubber lipid concentration of 60%) of southern right whales to be 202.6, 553.4, 1502.7 and 1867.2 MJ day⁻¹ for juveniles, adults, and pregnant and lactating females, respectively. Marine mammals are also exposed to a multitude of anthropogenic stressors (e.g. shipping, naval activities, entanglements with fishing gear, oil and gas exploration and whale-watching activities; Knowlton et al., 2012; Rolland et al., 2012; Sprogis et al., 2023), which can have cumulative effects on the targeted population (National Academies, 2017). These stressors can alter the behaviour of cetaceans (Arranz et al., 2021; Carstensen et al., 2006; Goldbogen et al., 2013; Senigaglia et al., 2016), with repeated disturbance potentially leading to long-term negative effects on individual vital rates and population dynamics (Bejder et al., 2006; Christiansen and Lusseau, 2015; New et al., 2014; Pirotta et al., 2018). With behavioural disturbance often being measured as changes in respiration rate and/or swim speed (Christiansen et al., 2014a; Sprogis et al., 2020a,b), our cost per breath metrics, which were 0.70, 1.41, 1.56 and 1.65 MJ breath⁻¹ for juveniles, adults, and pregnant and lactating females, respectively, provide a direct link among behavioural changes (changes in respiration rate and/or swim speed), bioenergetics and body condition. These metrics are likely to be most accurate for NPNL adults, which have low somatic growth costs (in comparison to calves and juveniles) (Christiansen et al., 2022b) and do not carry the added cost of reproduction (in comparison to pregnant and lactating females). In support of this, our two modelling approaches (respiration rate versus body condition loss) yielded similar estimates of FMR and TEE for NPNL adults. Further, while our FMR and TEE estimates rely on numerous assumptions relating to tidal volume and oxygen extraction (for the respiration rate-based estimates) or blubber density and energy content (for the body condition-based estimates), the body condition per breath estimates are based on direct estimates of body condition loss and respiration rate, and hence offer a direct link between behaviour and body condition. For capital breeding mysticetes, body condition plays a central role in reproduction (Christiansen et al., 2014b, 2016a, 2018;

Lockyer, 2007; Williams et al., 2013). For right whales, Christiansen et al. (2018) showed that the body condition of lactating females at the time of birth determines the amount of energy they can invest in their calf, and its subsequent growth rate. A reduction in female body condition due to an increase in FMR (measured through its respiration rate) can be directly related to this, so that the long-term consequences for calf growth and survival can be estimated. With the respiration rate and mass-specific FMR of right whales decreasing significantly with increasing body size, our study also highlights the importance of considering body size when assessing the impacts of anthropogenic disturbance on whales.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: F.C.; Methodology: F.C., K.R.S.; Formal analysis: F.C., M.G.; Investigation: F.C., K.R.S., M.L.K.N.; Resources: F.C., K.R.S.; Data curation: F.C.; Writing - original draft: F.C.; Writing - review & editing: K.R.S., M.L.K.N., M.G., L.B.; Visualization: F.C.; Project administration: F.C., K.R.S.; Funding acquisition: F.C., L.B.

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Data availability

All relevant data can be found within the article and its supplementary information.

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