Body condition and migration timing of east Australian humpback whales

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ABSTRACT: In order to exploit seasonally favourable habitats for feeding and breeding, humpback whales *Megaptera novaeangliae* undertake one of the longest migrations in the animal kingdom. Stored energy is crucial for a successful migration, but few studies have investigated the relationship between migration timing and body condition in baleen whales. Using unmanned aerial vehicles, we quantified the body condition of east Australian humpback whales. We collected data on 513 individuals (48 calves, 166 juveniles, 251 adults, and 48 lactating females) during their northbound and southbound migrations between June and October 2020. For adults and juveniles, we explored the loss of body condition between migration direction (north versus south) as well as the relationship of migration timing (day of year) and body condition. We found a significant loss in body condition between the northbound and southbound migrations for both adults (9.8%) and juveniles (18.3%). However, migration timing did not influence body condition for either reproductive class. Cow/calf pairs were analysed using relative calf length (percentage of maternal length) as a proxy for days postpartum. We found a positive curvilinear relationship between migration timing and calf body condition. However, lactating females showed no relationship between migration timing and body condition. Whilst body condition is important for capital breeding whales, the lack of a correlation found for adults and juveniles suggests that body condition is not the main driver of migration timing from feeding or breeding grounds. However, calf body condition may be a significant factor for the migration timing of cow/calf pairs.

KEY WORDS: *Megaptera novaeangliae* · Baleen whale · Photogrammetry · Unmanned aerial vehicle · UAV · Fat reserves · Capital breeder

1. INTRODUCTION

Migration is a seasonally driven behaviour that enables populations to relocate synchronously between alternately favourable conditions for breeding and/or foraging, in a way that maximises ecological fitness (Dingle 1996). Humpback whales *Megaptera novaeangliae* undertake one of the longest migrations among mammals (Stone 1990, Rasmussen et al. 2007) in order to exploit food-rich waters in higher latitudes

during the summer, and warmer lower latitudinal waters during the winter to breed (Chittleborough 1965, Robbins et al. 2011, Andrews-Goff et al. 2018). Feeding is largely absent during the migration and time spent on the breeding grounds, with individuals relying on previously stored energy reserves (i.e. 'capital') obtained on the feeding grounds. This annual migration has been widely studied in both the northern and southern hemispheres (Chittleborough 1965, Dawbin 1966, Craig et al. 2003, Stevick et al.

2003, Rasmussen et al. 2007, Rizzo & Schulte 2009, Jackson et al. 2014). However, migration behaviour is complex, involving variation between and within species, inter- and intra-seasonally, as well as differences among age, sex, and reproductive classes (Swartz 1986, Craig et al. 2003, Burns et al. 2014, Thomisch et al. 2016).

In migratory capital breeding mammals, migration is an important life cycle event given the energetic trade-off between energy acquisition and reproduction (Stephens et al. 2009, Irvine et al. 2017). Baleen whales store most of their energy as fat (lipid) reserves in their blubber, bones, muscle, and viscera tissues, which consequently can be highly variable in both weight and biochemical composition (Brodie 1975, Lockyer 1987a, Higgs et al. 2011). Seasonal variations in stored energy resulting from periods of intense feeding and fasting result in seasonal changes in the relative energy reserves of an individual, also known as body condition (Lockyer 1987a, Niæss et al. 1998). The body condition of an animal can be expressed by any physiological index that represents the energy stores of an individual relative to its structural size (Peig & Green 2010). Some common metrics used for body condition in baleen whales include body girth (Lockyer 1987b, Vikingsson 1990, Haug et al. 2002), blubber thickness (Vikingsson 1990, Miller et al. 2011), blubber volume (Christiansen et al. 2014), lipid concentration (Kershaw et al. 2019, Aoki et al. 2021), body surface area (Soledade Lemos et al. 2020), body volume (George et al. 2015, Christiansen et al. 2018), and body mass (Lockyer 1987b, Næss et al. 1998), often in relation to the body length (structural size) of the animal. Sufficient energy reserves need to be acquired to cover the basic metabolic requirements of fasting individuals, as well as additional energetic costs associated with demanding life-history stages such as late pregnancy and early lactation (Parry 1949, Braithwaite et al. 2015). Consequently, the amount of stored energy a humpback whale acquires from the feeding grounds dictates the ability of individuals to withstand longer periods of fasting, as well as the reproductive potential of mature females (Møller & Saino 1994, Cotton et al. 2006, Moya-Laraño et al. 2008, Williams et al. 2013). The body condition of an individual should hence determine the duration an animal is able to reside on the breeding grounds, and consequently, the migration timing to and from the breeding grounds. This is especially relevant for cow/calf pairs where time postpartum spent on the breeding grounds is important for calves to develop muscle mass to aid migration back to the feeding grounds.

Compared to income breeding marine mammals, like sperm whales *Physeter macrocephalus*, an equivalent length humpback whale carries 32–75% more body lipids (Irvine et al. 2017). The comparatively higher amount of stored energy in humpback whales is likely due to the high energetic cost of migration and reproduction which occurs during a prolonged period of fasting. For baleen whales, the amount of energy reserves an individual deposits will vary depending on reproductive status and time of year (Lockyer 1981, Perryman & Lynn 2002, Miller et al. 2012).

Despite the importance of body condition for migration and reproductive success in humpback whales, few studies have explored the relationship between migration timing and body condition. Historical whaling data have revealed that pregnant humpback whales that arrive in Australian waters later during the migration season carry larger energy stores compared to those arriving earlier (Irvine et al. 2017). Therefore, pregnant females may time migration according to individual gestation timing whilst prioritising energetic accumulation on the feeding grounds. The migration timing of adult males may be driven by a trade-off between energy accumulation and maximising the time spent on the breeding grounds to increase mating opportunities (Irvine et al. 2017). However, juvenile humpback whales are not yet sexually mature, and their migration time might therefore not be driven by the need to maximise reproductive success, but by other bioenergetic (e.g. thermoregulatory benefits) or ontogenetic (e.g. behavioural development) factors (Craig et al. 2003). Quantifying the energy stores of different reproductive classes of whales and how they may be influenced by the timing of migration, can provide valuable insights into the time investment trade-off between energy accumulation and reproduction.

The aim of this study was to investigate the relationship between body condition and migration timing in humpback whales. We used unmanned aerial vehicles (UAVs) to assess the morphometric body condition of migrating humpback whales off the east coast of Australia (Breeding Stock E1, BSE1) to (1) quantify the change in body condition between the northern migration (whales travelling from their Antarctic feeding grounds northward to their breeding grounds near the Great Barrier Reef Marine Park, GBRMP) and southern migration (whales travelling from the GBRMP down to Antarctica) for different reproductive classes, i.e. calves, juveniles, adults, and lactating females; and (2) determine whether the timing of migration (the day of the year an individual

migrates past northern New South Wales) influences body condition of humpback whales.

Regarding the Objective (1), above, we hypothesised (i) a decrease in body condition between the north- and southbound migrations for all reproductive classes with the exception of calves, (ii) the amount of body condition loss to be different for each reproductive class, and (iii) lactating females to lose the most body condition followed by non-lactating adults and juveniles.

Regarding the Objective (2), above, we hypothesised (i) that migration timing will significantly influence the body condition for all reproductive classes on the northern migration, with individuals migrating earlier expected to be in poorer body condition compared to those migrating later. However, during the southern migration, we expected to see different relationships for each reproductive class. For adults (males, resting females, and early-pregnant females), we hypothesised (ii) that migration time would have no effect on body condition due to confounding effects of sex and reproductive status. For juveniles, based on the thermoregulation hypothesis (where smaller individuals have a larger surface area to volume ratio, and therefore have more relative area to lose heat from), we hypothesised (iii) a significant decline in body condition with migrating timing. For cow/calf pairs, we expected (iv) to see calves in better body condition migrating later with a similar condition reflected in the lactating females.

2. MATERIALS AND METHODS

2.1. Study population

Each austral winter between May and November, the southern hemisphere population of humpback whales from BSE1 migrates from feeding grounds in Antarctica (feeding area V, 130° E−170° W, 59−68° S) to breeding grounds in the GBRMP (Forestell et al. 2003, Smith et al. 2012, Bettridge et al. 2015). Whaling significantly reduced the population of BSE1, with lower estimates of a few hundred individuals in the 1960s (Jackson et al. 2008). However, the cessation of commercial whaling in Australian waters in 1963 has allowed the population to recover. Dedicated population surveys, which began in the 1980s, have indicated a long-term average increase in the population at a rate of 10.9% yr^{-1} (Noad et al. 2019). The most recent population survey of BSE1 (in 2015) estimated the population at 24 545 ($\pm7.4−8.4\%$) individuals (Noad et al. 2019). The east coast of Australia provides an ideal location to study humpbacks along their migratory route, with approximately 90% of individuals travelling within 10 km of the coastline when passing Cape Byron (Paton 2016).

2.2. Study site

Surveys were conducted in northern New South Wales (NSW) from 2 land-based sites along the coastline, as well as from a commercial whale-watching vessel, hired for the purposes of this study. Flights from land were conducted from Ballina Head and Evans Head (Fig. 1). The commercial vessel departed from Brunswick Heads, and was used to survey farther offshore to help mitigate data sampling biases associated with sampling only near-shore individuals (Fig. 1). Sampling from the research vessel occurred up to 18 km from the coast, between 28° 21′ 36″ S, 153° 45′ 0″ E and 28° 39′ 36″ S, 153° 45′ 0″ E, spanning approximately 100 km^2.

2.3. Data collection

The research team was composed of 2 to 3 people, including a UAV pilot, a spotter/data recorder, and often a dedicated person to hand launch and retrieve the UAV when operating from the vessel. Zenithal (from directly above) 4K ultra-high definition video recordings were made of the dorsal side of surfacing humpback whales between 11 June and 22 October 2020 using a DJI Phantom 4 Pro UAV (weight 1388 g, diagonal size 350 mm), which had an integrated camera sensor. The UAV was launched from either the dedicated research vessel or the headland and flown 20−40 m in altitude toward the whale. Once above the whale, the UAV descended to approximately 20 m altitude to record videos from above the whale.

2.4. Data processing

Data were generated using definitions and protocols described by Christiansen et al. (2018, 2020). From the UAV videos, a minimum of 1 still frame photograph was extracted for each whale in the group. An ideal photograph for aerial photogrammetry is represented by a whale lying flat at the surface with its dorsal side clearly visible. The body should be non-arching and non-rolled, and the body contour clearly distinguishable to allow accurate measurements of body length and width. Each photograph was quality
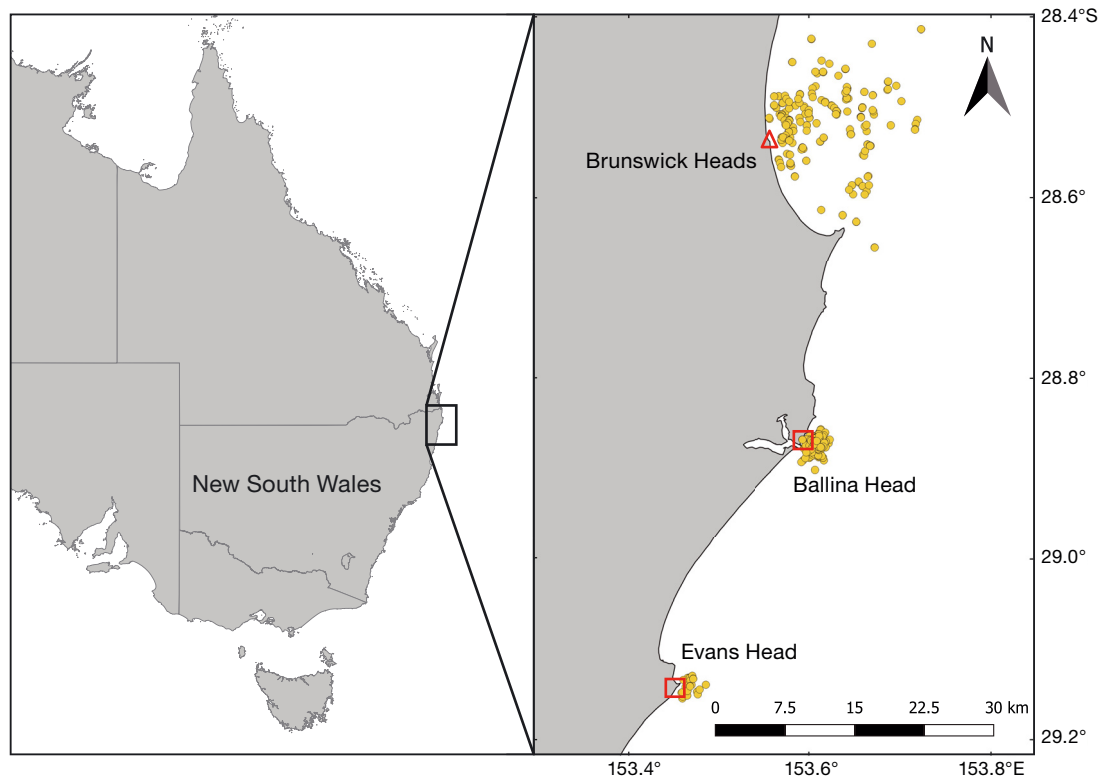
Fig. 1. Three sampling locations in northern New South Wales, including the land sites at Ballina Head and Evans Head (unmanned aerial vehicle take-off points denoted by the red squares), as well as the vessel departure location at Brunswick Heads (denoted by the red triangle). Yellow dots indicate the locations of sampled (photographed) humpback whales used in this study

graded (1: good, 2: medium, 3: poor) based on camera focus, body posture (straightness of the body, degree of body roll, degree of body arch, body pitch), and length and width measurability (ability to identify the body contour to measure body length and width, respectively). Images that scored a 3 in any variable or a 2 in both arch and pitch, pitch and roll, or arch and roll were excluded from the analysis.

Individuals were classified into 1 of 4 reproductive classes (calves, juveniles, adults, and lactating females). Individuals <11.2 m were classified as juveniles; those ≥11.2 m were classified as adults (Chittleborough 1955). Lactating females and calves were determined by their close and consistent association with one another and by their relative size (calves <2/3 body length of mothers; Christiansen et al. 2016). Apart from lactating females, differentiation between sexes was not possible, and hence the adult reproductive class comprised males, resting females (non-pregnant/non-lactating), and newly pregnant females (females that became pregnant during the study season).

For each whale (video still frame), we measured total body length (from the tip of the rostrum to the notch of the tail fluke), and body width (Fig. 2). Width measurements of whales from the images were made perpendicular to the body axis and at 5% intervals along the entire body, excluding 0 and 100% of the body length (Fig. 2) (Christiansen et al. 2016). The length and width measurements were converted from pixels on a still image to absolute size (in metres) by scaling each still frame. This was done by taking into account the known altitude of the UAV, camera sensor size, focal length, and image resolution (Christiansen et al. 2018).

2.5. Body length, volume, and condition

The body condition of individual humpback whales was estimated from the residual of the log-linear relationship between body volume and body length (Christiansen et al. 2018). First, body volume was calculated from the body width, length, and height data following the procedures of Christiansen et al. (2019). Height data were obtained using height-to-width ratios calculated from data collected by Christiansen et al. (2020). Each whale was modelled using small ellipses to form the cross-section of its body. The ellipses varied in width and height ac-

cording to each 5% segment along the whale body. The width to height ratio was calculated for each segment using data from whales with both a dorsal (width) and lateral (height) image. The volume (V) for each body segment (ellipses) was calculated using the following formula (Christiansen et al. 2019):

$$V_{s,i} = BL_i \times 0.05 \times$$

$$\int_0^1 \pi \times \frac{W_{A,s,i} + (W_{P,s,i} - W_{A,s,i}) \times x}{2} \times \frac{H_{A,s,i} + (H_{P,s,i} - H_{A,s,i}) \times x}{2} dx \quad (1)$$

where s is the segment being measured for whale i, BL is the total body length of whale i, $W_{A,s,i}$ and $W_{P,s,i}$ are the anterior and posterior width measurements, respectively, and $H_{A,s,i}$ and $H_{P,s,i}$ are the anterior and posterior height measurements, respectively. We used a linear interpolation of both body width and height from 0–5% BL (tip of the rostrum) and from 85–100% BL (tail region). The total body volume ($BV_{Total,i}$) of whale i was then calculated by the summation of all body segments:

$$BV_{Total,i} = \sum_{s=1}^{20} V_{s,i} \quad (2)$$

The body condition (BC) was then calculated using the BV_{Total} for each whale using the following formula (Christiansen et al. 2018):

$$BC_i = \frac{BV_{Obs,i} - BV_{Exp,i}}{BV_{Exp,i}} \quad (3)$$

where $BV_{Obs,i}$ and $BV_{Exp,i}$ are the observed (measured) and expected (average) body volume of whale i measured in m³. The expected body volume for each whale was estimated from the linear log–log relationship between body volume and total body length:

$$\log(BV_i) = \alpha + \beta \times \log(BL_i) \quad (4)$$

where BV_i is the expected body volume of whale i and BL_i is the measured body length for whale i.

2.6. Data analysis

The cost of residing on the breeding grounds was quantified by comparing the body condition between the northbound (North, May–August) and southbound (South, August–November) migrations for each reproductive class (calves, juveniles, adults, and lactating females). Data were analysed using linear regression models (LMs) in R v4.0.4 (R Core Team 2021) (Model 1 LM: body condition [BC] ~ migration direction, subset = reproductive class). A separate model was used for each reproductive class, represented in the model under 'subset'. The migration direction (North or South), was determined for each sampled whale considering the date of the sightings, and the predominant direction of travel by the individual. For adults and juveniles, the relationship between body condition and migration timing (day of the year) was quantified using LMs with the northbound and southbound migrations analysed separately (Model 2 LM: BC ~ day of the year, subset = reproductive class and travel direction). Instead of day of the year, migration timing for cow/calf pairs was analysed using the relative body length of the calf (CBL = calf body length/maternal body length) as a proxy for days postpartum, since the date of birth varied between individual calves and calves grew in body length over the breeding season. Lactating females were analysed using LMs (Model 3 LM: BC ~ CBL, subset = reproductive class), whilst calf body condition was analysed using a generalised additive model (GAM) and a Gaussian family (Model 1 GAM: BC ~ smooth spline [%CBL to female body length], subset = reproductive class). Models were visually examined for each reproductive class and were validated and tested for potential violations of the assumptions of normality, homoskedasticity, and normality of residuals.

3. RESULTS

The research effort spanned 68 survey days and was divided between 3 survey locations, with 44 days at Ballina Head, 7 at Evans Head, and 17 on the research vessel (departing from Brunswick Heads). A total of 699 still images of individual humpback whales were extracted from the videos. After assessing imagery and filtering the data based on picture quality, a total of 513 individual whales were used in the analysis (237 North and 276 South), including 48 calves (7 North and 41 South), 166 juveniles (100 North and 66 South), 251 adults (123 North and 128 South), and 48 lactating females (7 North and 41 South) (Table 1). Adults and juveniles were sampled throughout the data collection period, with cow/calf pairs being sampled from early July (Fig. S1).

3.1. Body length, volume, and condition

Total body length of humpback whales ranged between 3.7 and 16.2 m (Table 2). Calves varied in

Table 1. Number of individual humpback whales of each reproductive class sampled at each survey location included in the analysis

Reproductive class	Ballina Head	Evans Head	Research vessel	Total
Calves	24	6	18	48
Juveniles	95	3	68	166
Adults	134	7	110	251
Lactating females	24	6	18	48
Total	277	22	214	513

length between 3.7 and 7.9 m, juveniles between 7.9 and 11.2 m, adults between 11.2 and 16.2 m, and lactating females between 10.8 and 15.1 m. There was a significant curvilinear (exponential) relationship between body length and body volume, with the log-log relationship showing a strong linear relationship ($F_{1,511}$ = 1634, p < 0.01, R^2 = 0.970) (Fig. 3). All whales followed a similar body width profile along the body axis, measured at 5% increments (Fig. S1 in the Supplement, www.int-res.com/articles/suppl/m692 p169_supp.pdf). The widest point for juveniles, adults, and lactating females was at 45% body length down the body axis, whereas calves were widest at 40% body length (Fig. S2). The minimum, maximum, and median body condition and body lengths for individuals used in the analysis were derived for each sample location (Fig. S3). The relationship of absolute body length of cow/calf pairs was analysed, with calf body length showing a significant relationship with maternal body length ($F_{1,46}$ = 6.63, p = 0.01, R^2 = 0.10). This relationship showed that longer (and potentially older) females had longer calves (Fig. S4). In addition, relative calf length (% of maternal length) was correlated with day of year, with longer (potentially older) calves migrating later ($F_{1,46}$ = 29.34, p < 0.01, R^2 = 0.37) (Fig. S5).

3.2. Changes in body condition between the northbound and southbound migrations

There was a significant loss in body condition between the north- and southbound migrations for adults ($F_{1,249}$ = 42.37, p < 0.001) and juveniles ($F_{1,164}$ = 107.8, p < 0.001) (Fig. 4). The small number of observations of lactating females and calves during the northbound migration prohibited a statistical comparison for these reproductive classes. Adults lost approximately 9.8 percentage points in body condition between the north and southbound migrations (Fig. 4). Adults migrating north were approximately 6.6 ± 0.01% (SE) above the total mean body condition of the whole sample population. This dropped to 3.2 ± 0.01% below the mean body condition during the southern migration. Juveniles lost approximately 18.3 percentage points of their body condition from the northbound (8.2 ± 0.01%) to the southbound migration (−10.1 ± 0.01%) (Fig. 4).

3.3. Influence of migration timing on body condition

We found no statistical evidence to support a relationship between migration timing (day of the year) and body condition for adults ($F_{1,121}$ = 2.49, p = 0.117) during the northbound migration (Fig. 5). The model showed potential weak evidence for juveniles to have declining body condition with day of the year during the northbound migration (Fig. 5). However, this was not statistically significant at a significance level of α = 0.05 ($F_{1,98}$ = 3.79, p = 0.054). There was also no statistical evidence to suggest that migration timing of adults ($F_{1,126}$ = 0.194, p = 0.660) and juveniles ($F_{1,64}$ = 0.191, p = 0.663) affects their body condition during the southbound migration. Similarly,

Table 2. Range (with mean ± SD) of body length, body volume, body condition, and body width at the widest point for different reproductive classes of humpback whales sampled on the east coast of Australia. Sample sizes (n) are also shown. Total n = 513 whales

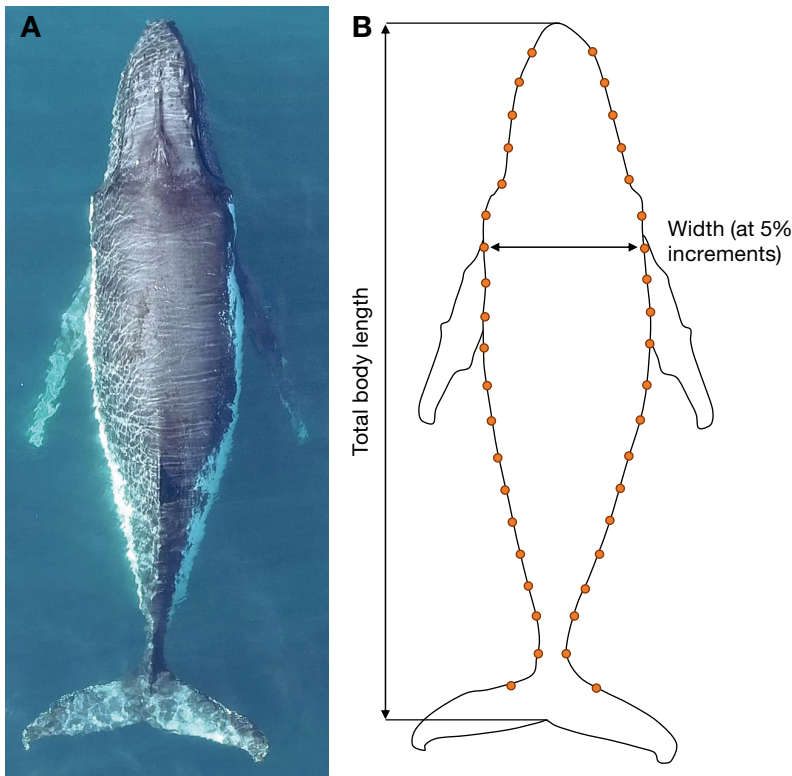| Reproductive class	n North	n South	Body length (m)	Body volume (m^3)	Body condition	Width at widest point (m)
Calf	7	41	3.7–7.9 (5.9 ± 0.81)	0.7–7.4 (3.2 ± 1.2)	−0.25 – 0.34 (−0.01 ± 0.12)	0.66–1.60 (1.17 ± 0.17)
Juvenile	100	66	7.9–11.2 (10.1 ± 0.83)	6.7–28.8 (16.1 ± 4.2)	−0.29 – 0.40 (0.01 ± 0.14)	1.37–2.61 (1.97 ± 0.22)
Adult	123	128	11.2–16.2 (12.7 ± 1.05)	16.9–64.9 (32.8 ± 8.7)	−0.26 – 0.46 (0.02 ± 0.13)	1.97–3.26 (2.51 ± 0.25)
Lactating	7	41	10.8–15.1 (12.8 ± 1.1)	17.45–59.9 (32.9 ± 9.2)	−0.23 – 0.32 (−0.01 ± 0.12)	1.99–3.09 (2.48 ± 0.24)
Total	237	276	3.7–16.2	0.7–64.9	−0.29 – 0.46	0.66–3.26

Fig. 2. (A) Example of an unmanned aerial vehicle-derived aerial photograph of a humpback whale from this study, and (B) the positions of measurements taken to assess body condition
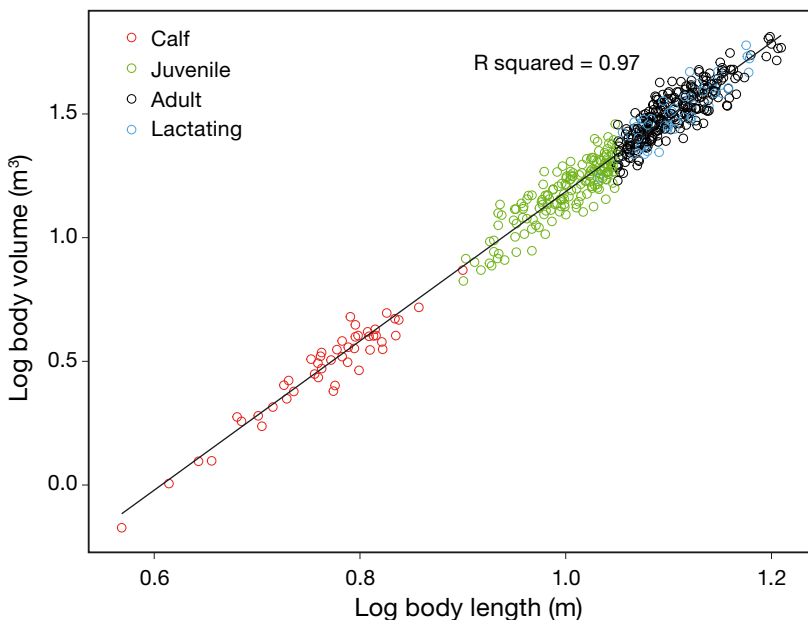

Fig. 3. Log-log relationship between body volume and body length for each reproductive class of breeding stock E1 humpback whales; n = 48 calves, 166 juveniles, 251 adults, and 48 lactating females

there was no evidence to support migration timing (relative calf length as a proxy for days postpartum) of lactating females affecting their body condition ($F_{1,46}$ = 3.84, p = 0.055) (Fig. 6). However, calves showed a significant curvilinear relationship, where those migrating with a body length approximately 40–50% that of their mothers, were in significantly better body condition than earlier (<40%) or later (>50%) migrating calves ($F_{1,9}$ = 0.24, p = 0.001; Fig. 7).

4. DISCUSSION

We investigated the relationship between body condition and migration timing in BSE1 humpback whales on the east coast of Australia. We recorded a significant loss in body condition for both adults and juveniles between their northern and southern migration. In addition, we found no evidence that the timing of migration influences body condition for adult, juvenile, and lactating female humpback whales for either migration direction (north or south). However, calves showed a significant non-linear relationship with body length relative to that of their mother (a proxy for migration timing postpartum) and body condition. Calves migrating past northern NSW with a body length between 40 and 50% of the maternal body length were on average in better body condition than calves migrating past with <40% or >50% of the maternal body length.

It is worth noting that the body condition metric used in this study was scaled against the body length of the animals, which means that measurement errors in body length should not influence the estimate of body condition. However, given that length is used as a threshold to determine adults and juveniles, it is likely that some adults were misclassified as juveniles and vice versa. Similarly, some pregnant females may have been misclassi-
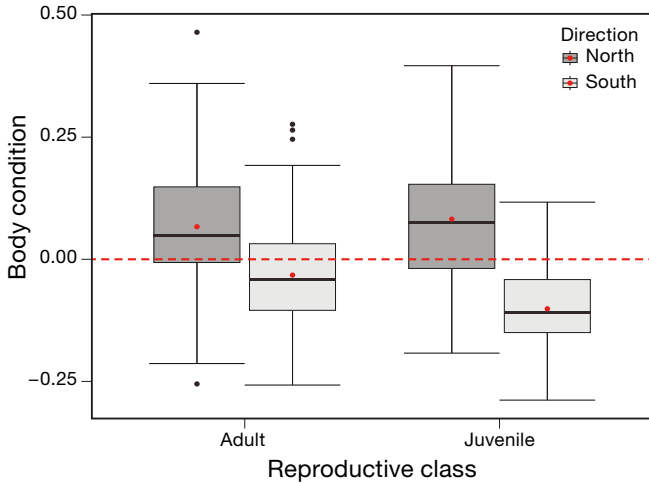
Fig. 4. Comparison of the body condition for humpback whale adults (n = 251) and juveniles (n = 166) during the northbound (dark grey) and southbound (light grey) migrations of breeding stock E1. The dashed red line indicates the average body condition (BC = 0) of the sample population, with the red dots indicating the means for each reproductive class and migration direction. The box indicates the upper and lower quartile, the black solid line represents the median body condition for each reproductive class, the whiskers show the maximum and minimum ranges of body condition, and black dots mark outliers

fied as juveniles during the northern migration. The lowest body length for a lactating female recorded in this study was 10.8 m, which is below the adult threshold of 11.2 m. The smallest sexually mature female humpback whale from whaling records presented by Chittleborough (1965) was 10.5 m; therefore, measurements of sexually mature whales under this length will most likely be due to measurement error or error in height recorded. In the absence of more recent data on the mean body length threshold of humpback whales reaching sexual maturity, whaling data provide the most accurate information currently available.

4.1. Adults

We found a significant decrease in body condition between the northbound and southbound migrations for adults (9.8%). This loss in body condition was expected given the high energetic cost of reproduction in female and male humpback whales while on the breeding grounds (Lockyer 1981, Oftedal 1993, Stephens et al. 2009). A similar loss in body condition
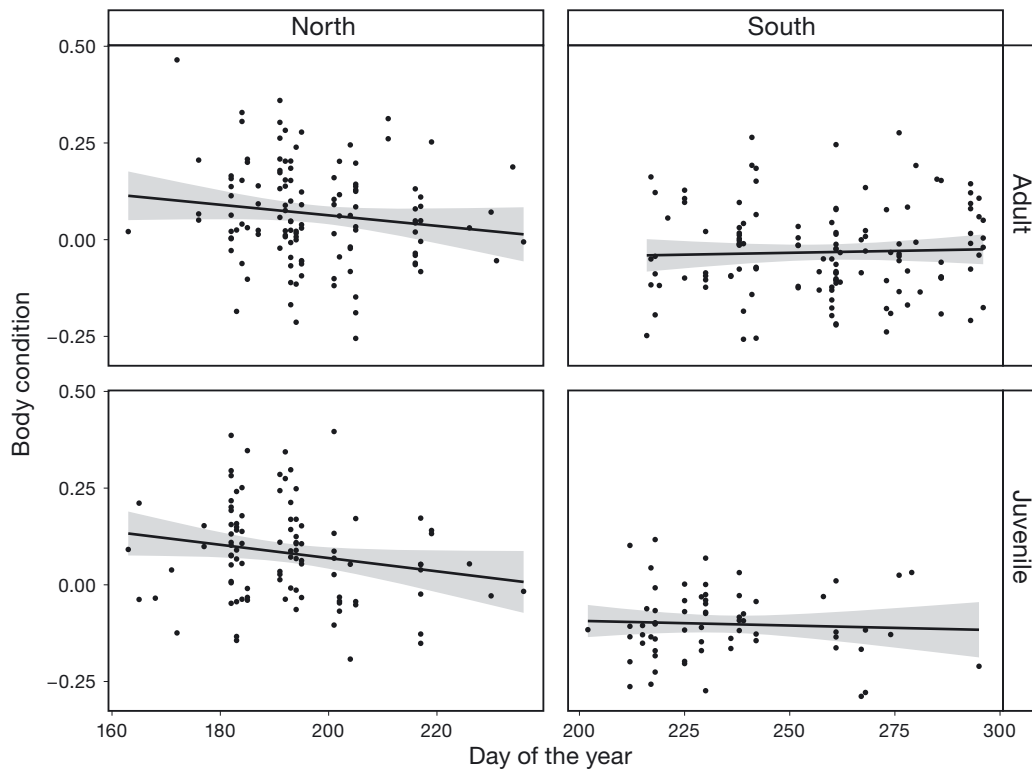

Fig. 5. Linear models showing the relationship between body condition and migration timing (day of the year) during the northern (left column) and southern (right column) migration for humpback whale adults (n = 251, top row) and juveniles (n = 166, bottom row). The solid black lines represent the predicted values of the fitted linear models, with the 95% confidence intervals represented by the grey shaded areas. None of the linear models was statistically significant
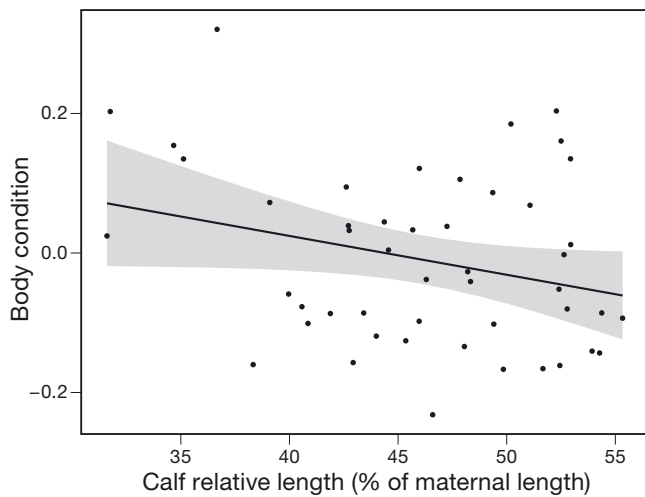
Fig. 6. Body condition and migration timing (i.e. calf relative body length) for lactating humpback whale females sampled in northern New South Wales (n = 48). The solid black line represents the predicted values of the fitted linear model, with the 95% confidence interval represented by the grey shaded area. The relationship was not statistically significant
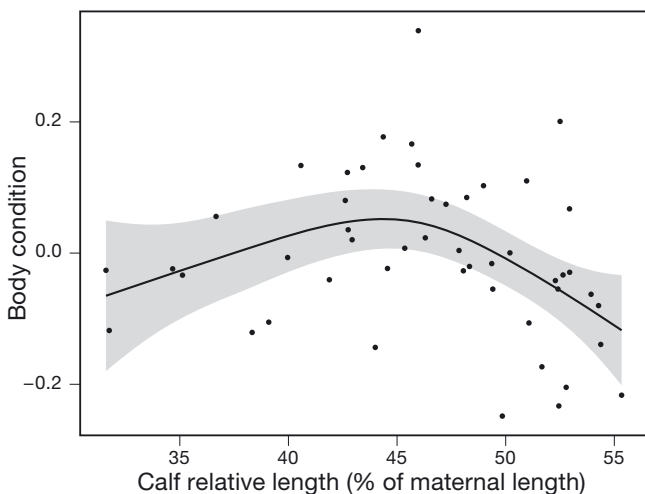

Fig. 7. Body condition and migration timing (i.e. calf relative body length) for humpback whale calves sampled in northern New South Wales (n = 48). The solid black line represents the predicted values of the fitted generalised additive model, with the 95% confidence interval represented by the grey shaded area

over a period of fasting has been well documented in other mammals (Lockyer 1981, Atkinson & Ramsay 1995, Champagne et al. 2012), including baleen whales (Perryman & Lynn 2002, Bradford et al. 2012, Miller et al. 2012, Christiansen et al. 2016, Soledade Lemos et al. 2020). The loss in body condition recorded during this study is similar to what has been recorded for Stock D humpback whales (14.5%) of Western Australia (WA), between early (northbound)

and late (southbound) migratory phases (Christiansen et al. 2020). In addition, a 20% decrease in oil yields was recorded at Carnarvon whaling station in northwest WA between humpback whales caught on their northern migration compared to those on the southern migration (Chittleborough 1965). The slightly smaller loss in body condition reported in the present study may be a result of differences in relative sampling position on the migratory route. In WA, data were collected farther south of the breeding grounds compared to this study, which may explain the larger loss in body condition. However, Carnarvon whaling station, which recorded the largest decrease, was the closest location to the respective breeding grounds of the 3 studies, approximately 1000 km south. Therefore, relative position of sampling on the migratory route would not explain this difference. Rather, records from Carnarvon whaling station may include all reproductive classes, including late-term pregnant females in good body condition and females approaching the end of lactation in poor body condition; the latter produced half as much oil yield as the former when caught at the same whaling location (Dawbin 1966). In addition to blubber, bones may have also been processed and oil extracted, potentially contributing further to the larger yield in oil recorded at Carnarvon (Ivashchenko et al. 2011). Moreover, there might not be a perfect linear relationship between oil yields and body condition, since a whale could be catabolising tissue lipids without it being reflected in the morphometric body condition of the animal (Christiansen et al. 2020). Therefore, the overall lipid loss may be greater than loss in morphometric body condition alone, which may explain the difference in body condition loss compared with the present study.

Although humpback whales are thought to generally fast during migration and while on the breeding grounds, significant feeding opportunities have been recorded during the southern migration on the east coast of Australia (Stamation et al. 2007, Pirotta et al. 2021). Feeding behaviour during migration has been recorded in other humpback whale populations, including the east coast of America, South Africa, Brazil, Dominican Republic, Ecuador, Chile, and Mexico (Baraff et al. 1991, Gendron 1993, Swingle et al. 1993, Best et al. 1995, Danilewicz et al. 2009, De Sá Alves et al. 2009, Barendse et al. 2010, Findlay et al. 2017, Siciliano et al. 2019, García Cegarra et al. 2021). This raises the possibility of revising this traditional model of feeding and fasting for at least some humpback whale populations (Eisenmann et al. 2016). The exact role and extent that feeding during

migration has on the energetic balance of humpback whales remains largely unknown. However, whales may be able to meet up to 3.4 times their daily energetic requirements when they suspend migration for opportunistic feeding (Andrews-Goff et al. 2018). Significant opportunities to replenish energy reserves may influence changes in body condition. The opportunistic feeding behaviour of humpback whales along the Australian east coast has been primarily observed during the southern migration about 1000 km south from the location of this study (Gill et al. 1998, Stockin & Burgess 2005, Gales et al. 2009, Owen et al. 2015). Although occasional feeding opportunities may provide additional energy to complete the final, and arguably more demanding, section of the migration, these are likely to have little influence on the results of this study.

We found no evidence to support migration timing in adult humpback whales being influenced by their body condition. However, migration timing of North Atlantic humpback whales has been found to be influenced by their feeding ground origin (Stevick et al. 2003). Localised environmental variables within feeding grounds can influence the amount of stored energy or body condition an individual can accumulate. The humpback whales that winter (breed) in the West Indies come from 5 main feeding areas, including Gulf of Maine, eastern Canada, Greenland, Iceland, and Norway (Stevick et al. 2003, Kennedy et al. 2014). The arrival and departure time of individuals in the West Indies was strongly influenced by their respective feeding areas, where those feeding in the Gulf of Maine and eastern Canada arrived and departed significantly earlier than those travelling from Greenland, Iceland, and Norway (Stevick et al. 2003, 2018). Humpback whales exhibit strong site fidelity to both their breeding and feeding grounds (Calambokidis et al. 2001, Barendse et al. 2013, Wenzel et al. 2020). Southern hemisphere humpback whales feed in 6 identified feeding areas, with whales showing strong site fidelity in each area (Chittleborough 1959, IWC 1999). BSE1 whales feed within feeding area V in Antarctica, spanning 130°E–170°W, 59°–68°S (Bettridge et al. 2015). However, fine-scale movement within this area is poorly understood. With other populations showing site fidelity to feeding areas on a smaller spatial scale (Barendse et al. 2013), there is a potential for this to occur within Antarctic feeding areas. This would cause different migration distances for the various individuals that comprise BSE1, and potentially affect migration timing perceived from the northern NSW study sites. Prey type and prey availability at different feeding sites are also likely to influence the amount of energy reserves an individual may gain during the feeding season, thus creating a mix of individuals migrating at different times with various body conditions.

During the southbound migration, the time at which an individual adult whale passed northern NSW did not influence its body condition. Sex determination of adults (apart from lactating females) was outside the scope of this study, and therefore some adults that migrated earlier may have been newly pregnant females. A newly pregnant female will have different strategies for maximising reproductive success (Craig et al. 2003), and thus would be more likely to conserve as much energy as possible during the breeding season. Residency times of BSE1 whales on their breeding grounds in the GBRMP were recorded to be an average of 2 mo (Burns et al. 2014). Males showed a longer mean residency time compared to females (Burns et al. 2014), supporting the hypothesis that males may seek to maximise breeding opportunities by spending more time on their breeding grounds (Craig et al. 2003). This difference in life history strategies between adult males and females may have obscured the relationship between body condition and migration timing for adults seen in this study.

4.2. Juveniles

Juveniles were observed to decline in body condition between the northbound and southbound migrations. Juvenile humpback whales lost more body condition (18.3%) during the breeding season compared to adults (9.8%). A similar pattern was also documented in juveniles in Breeding Stock D in WA (Christiansen et al. 2020), which lost 28.5%. The authors predicted that younger, smaller juveniles, possibly newly weaned and still fat from their mothers' milk, might have been overrepresented in the 'early phase' (northbound migration), whereas the 'late phase' (southbound migration) captured a more accurate snapshot of juvenile body condition, thus creating a large drop in body condition that may not be representative of the juvenile class. In the present study, we collected data over the entire migration period and still found the same pattern, suggesting that the larger loss in body condition of juveniles was not due to sampling biases.

The relatively large loss of body condition in juveniles was not expected, since juveniles do not carry the added cost of reproduction (Oftedal 1993, 1997).

However, juvenile humpback whales are still growing in length to reach sexual maturity, and this growth may be an important factor when comparing energetic requirements between reproductive classes. The mass-specific energetic requirement for juvenile North Atlantic right whales *Eubalaena glacialis* was estimated to be considerably higher than that needed for adult males and non-reproductive females (Fortune et al. 2013). In addition, immature minke whales *Balaenoptera acutorostrata* showed no seasonal variation in body condition (i.e. blubber volume) over the feeding season (Christiansen et al. 2013), suggesting that juveniles may use any excess energy gained from feeding for growth. We found that the body volume, and hence mass, of humpback whales increased exponentially with body length, and therefore adults are substantially heavier compared to juveniles. According to 'Kleiber's Law', the mass-specific metabolic rate of an animal decreases with increasing body size (Kleiber 1932). Based on this law, the relative (mass-specific) energetic cost of maintenance would be significantly higher for juveniles compared to adults. Since the body condition metric in our study accounted for the structural size of the whales, a larger loss in body condition of juveniles compared to adults would be expected. In combination with the required energy needed for growth, this may represent a substantial energetic cost for juveniles, which exceeds that of adult whales.

We found the potential for a weak influence of migration timing on body condition for juvenile humpback whales from BSE1, but this influence was just outside the 95% confidence interval, and therefore was not statistically significant. Residency times on feeding and breeding grounds for juveniles will not be influenced by trade-offs between reproduction and energy acquisition. Instead, juveniles may only be influenced by their limited energy reserves (Craig et al. 2003). Craig et al. (2003) concluded that the initiation of migration for humpback whales is most likely due to complex interactions between food availability on the feeding grounds, hormonal state, body condition, and photoperiod. However, based on the results of this study, body condition does not seem to be a major factor in determining the migration timing of humpback whales. Logically, if whales were to fall below a certain body condition threshold that would threaten their survival, they would leave the breeding grounds. However, since BSE1 represent a healthy (growing) population of humpback whales, most individuals were likely to be far away from this threshold.

4.3. Lactating females and calves

Calves showed a significant curvilinear relationship between body condition and migration timing (i.e. relative CBL), with early (CBL <40% of maternal length [ML]) and late (CBL >50% ML) migrating calves displaying significantly poorer body condition than those passing northern NSW between 40 and 50% ML. Calves increasing in both length and body condition throughout their migration was expected, since they are nursing on high caloric milk provided by their mothers (Oftedal 1997). However, how baleen whale calves prioritise between somatic growth (body length) versus fat deposition (body condition) has not been investigated in depth. Absolute body width is highly correlated to absolute body length, and the body condition of an individual is based on the relationship between the 2 variables. Consequently, calves that have grown in length but not increased in relative width are not necessarily thinner than shorter calves, they have simply grown in absolute size without their body condition changing. Therefore, at a certain length or width, calves may change where they prioritise their energy investment. Christiansen et al. (2016) found no temporal change in calf body condition of humpback whale cow/calf pairs in Exmouth Gulf, WA. The authors hypothesised that calves may prioritise growth in length over body condition in order to survive the long migration back to Antarctica. Growth in length will aid swimming abilities, swimming efficiency, and potentially predator avoidance, while an overall increase in body size (i.e. length) will reduce heat loss due to a reduction in the surface area to volume ratio (Sumich 2021).

Given the direct relationship between calf and maternal body condition (Christiansen et al. 2016, 2018), it was unexpected that no relationship between migration timing and body condition for lactating females was shown. Baleen whale maternal investment has been linked to female body condition at the time of birth, meaning that females in better body condition are able to increase their energetic investment (milk transfer) into calf growth rate (Christiansen et al. 2016, 2018). Furthermore, larger (i.e. longer) females were recorded to have significantly more energy reserves and also longer calves, once again being able to invest more energy and body volume into their calf (Christiansen et al. 2016, 2018). Therefore, one would expect the body condition of lactating females to be influenced by migration timing (i.e. CBL). Despite not finding a significant positive relationship during this study, the

model indicated weak evidence for such a trend. The migration timing of cow/calf southern right whale *E. australis* pairs in South Australia were influenced mostly by diurnal period, followed by calf size, sea surface temperature, and lastly maternal body condition (Dickeson 2018). The authors concluded that calf size, rather than maternal size, facilitates migration from breeding grounds.

Using relative calf length as a proxy for migration timing may introduce some errors due to maternal body length not reaching its maximum by the time of first parturition. These errors, however, will be minimal due to the significant effect of maternal body size on calf birth size (Christiansen et al. 2016, 2022). Data from this study support previous findings that maternal body length has a significant effect on calf length, with longer females having longer calves.

4.4. Conclusions and management implications

Stored energy acquired from feeding grounds fuels the energetic cost of migration and reproduction in capital breeding marine mammals. This stored energy dictates the ability of individuals to withstand long periods of fasting whilst enabling energetically demanding activities like breeding, calving, and lactation. This study used body condition as a physiological index to represent the amount of stored energy an individual carries relative to its structural size. When examining the relationship between migration timing and changes in body condition for different reproductive classes, juveniles lost the most body condition between their northbound and southbound migrations. This was potentially due to their high mass-specific metabolic rate and higher growth rate compared to adult whales. Calves were the only reproductive class whose body condition was significantly influenced by migration timing with early and late migrating calves in significantly poorer body condition than those migrating in the middle.

Despite the importance of body condition for reproduction and migration in capital breeding marine mammals, few studies have explored the relationship between migration timing and body condition. It is important to obtain information and monitor baleen whale energetics during migration and over their reproductive cycle to determine any adverse effects created by anthropogenic disturbances. Australian humpback whale populations have been making a remarkable recovery since the cessation of whaling (Noad et al. 2019), but significant threats remain. The increase in coastal development, industry practices,

and shipping around Australia pose a serious threat of not only injury and mortality due to vessel strikes, but also disturbance and displacement in key habitat areas (Clifton et al. 2007, Peel et al. 2018, Bejder et al. 2019). In addition, modification in prey availability and diversity have been observed in the Southern Ocean, the main feeding grounds of southern hemisphere humpback whales, as a result of climate change driven impacts, including ocean warming, ozone depletion, reduced sea ice, and environmental stress (Stammerjohn et al. 2008, Flores et al. 2012, Kawaguchi et al. 2013). Anthropogenic and climatic stressors can influence the amount of energy acquired on feeding grounds and impact energy usage during migration. This study provides valuable insight into the migration timing and energetic usage of east Australian humpback whales. The results of this study and similar studies are needed to develop and implement effective management strategies formulated to protect the nutritive condition, and ultimately population dynamics, of migrating animals.

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