

# Comparisons of morphometrics and body condition between two breeding populations of Australian humpback whales

Grace Russell<sup>A,\*</sup> , Fredrik Christiansen<sup>B</sup>, Andrew Colefax<sup>C</sup>, Kate R. Sprogis<sup>D</sup>  and Daniele Cagnazzi<sup>A</sup>

For full list of author affiliations and declarations see end of paper

**\*Correspondence to:**

Grace Russell  
Marine Ecology Research Centre, Southern  
Cross University, Military Road, East  
Lismore, NSW 2480, Australia  
Email: [g.russell.1@student.scu.edu.au](mailto:g.russell.1@student.scu.edu.au)

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## ABSTRACT

**Context.** The east and west coasts of Australia form the breeding grounds for two of the world's largest and fastest-growing populations of humpback whales (*Megaptera novaeangliae*). These populations show differences in mean lipid content, fatty acid profiles, and stable isotope values.

**Aims.** To determine whether these differences result in variation in nutritional health and physiology between populations, we quantified and compared the morphology, body condition and energetic requirements between the two populations. **Methods.** We used unmanned aerial vehicles to measure body morphometrics (residual of body volume vs length) of humpback whales from May to November in 2017, 2020 and 2021. **Key results.** Morphometric measurements were obtained from 973 humpback whales (119 calves, 249 juveniles, 486 adults, and 119 lactating females). Results showed that the two populations did not differ significantly in their morphology. The average body condition was significantly different for sexually mature reproductive classes, with adults and lactating females on the west coast having a lower body condition, by an average of 7.7 and 11.1 percentage points below the east coast population respectively. All reproductive classes, with the exception of calves followed a similar pattern in body condition loss through the breeding season. Calves on the east coast exhibited a curvilinear relationship with days post-partum, with early and late-migrating calves being in poorer body condition than were those migrating mid-season. In contrast, west coast calves did not significantly change their condition through the breeding season. **Conclusions.** The poorer body condition of sexually mature individuals in the west coast population is concerning, given the overall condition loss during a breeding season. This difference could be influenced by variations in sampling time; however, differences in feeding opportunities, climatic regimes and/or environmental variables may influence the ability of one population to acquire similar amounts of energy. **Implications.** The difference in body condition between these two humpback whale populations highlighted the need to assess populations individually, so as to develop representative levels that can be used for future conservation monitoring and management.

**Keywords:** Baleen whale, body condition, capital breeder, drones, *Megaptera novaeangliae*, morphology, photogrammetry, unmanned aerial vehicle (UAV).

## Introduction

Marine mammals face a host of environmental and anthropogenic threats that can affect the health and survival of individuals within a population (Doney *et al.* 2012; Evans and Bjørge 2013; Van Der Hoop *et al.* 2013; Sanderson and Alexander 2020). These threats, including anthropogenic noise, vessel strikes, fishing gear entanglement, pollution, overharvesting of prey, habitat degradation, and climate change, can have an influence on the fitness of an animal as well as an indirect influence by affecting ecosystem health and prey availability (Fortune *et al.* 2013; Peel *et al.* 2018; Tulloch *et al.* 2020; Kershaw *et al.* 2021). If ongoing and severe, the various anthropogenic and environmental disturbances can compound and cause alterations in behaviour or deplete the abundance of individuals in populations (Leaper *et al.* 2006; New *et al.* 2014; Williams *et al.* 2016; Stewart *et al.* 2021). Investigating a population nutritional status and body condition can provide an indication of ecosystem

health and population viability (Bonde *et al.* 2004; Bengtson Nash *et al.* 2018; Groszkreutz *et al.* 2019). Body condition is often used as a proxy for the relative energy reserves of individuals, which can affect fitness, somatic growth rates, fecundity and survivability (Lockyer 1990; Merilä and Svensson 1997; Lockyer 2007; Bradford *et al.* 2012; Castrillon and Bengtson Nash 2020).

Comparisons of body condition can be used to identify differences in prey availability, foraging success, and anthropogenic threats between among populations, and provide insights into recent changes in critical habitat, somatic growth rates, and calving (Goodman 1997; Rode *et al.* 2012; Ashton *et al.* 2015; Christiansen *et al.* 2020a). For example, the shorter body length and poorer body condition of southern resident killer whales than of the sympatric population Bigg's killer whales, has been linked to differences in the adaptive selection of prey and its differential availability (Kotik *et al.* 2023). Furthermore, a comparison of body condition across one population of the North Atlantic (*Eubalaena glacialis*) and three populations of southern right whales (*Eubalaena australis*) showed that the former is in a significantly poorer nutritional state, which may be contributing to the low reproductive rate and high mortality of the population (Christiansen *et al.* 2020a).

Most baleen whale populations undertake long-distance migrations from polar feeding areas to tropical breeding grounds (Chittleborough 1965; Dawbin 1966; Stone *et al.* 1990; Mikhalev 1997; Palsbøll *et al.* 1997; Jenner *et al.* 2001). This movement enables populations to exploit seasonally favourable habitats (Clapham 1996, 2001; Pallin *et al.* 2023). On the breeding grounds, humpback whales (*Megaptera novaeangliae*) rely primarily on stored energy acquired during the previous feeding season(s) to support their energetic needs. Because of this, physical (morphological) changes in stored energy can be observed over the course of their migration and breeding season (Perryman and Lynn 2002; Christiansen *et al.* 2016a; Soledade Lemos *et al.* 2020). In addition, temporal and spatial changes to prey availability due to climate change, climate regimes (i.e. El Niño Southern Oscillation, ENSO) or anthropogenic disturbances (i.e. over harvesting of prey) should be reflected in time spent on feeding grounds, prey choice and/or foraging locations, and therefore the body condition of individuals (Holyoake *et al.* 2012; Eisenmann *et al.* 2016; Owen *et al.* 2017; Bengtson Nash *et al.* 2018).

There are two breeding populations of humpback whales in Australia, one that migrates along the west coast and another that migrates along the east coastline, namely, Breeding stock D (BSD) and Breeding stock E1 (BSE1) respectively (IWC 2011). Both are believed to be among the largest breeding populations of humpback whales in the world, with current estimates exceeding 30 000 whales (Kent *et al.* 2012; Noad *et al.* 2019). The two populations are putatively discrete breeding populations and are considered to be largely separate. They feed in neighbouring areas in Antarctica, known as

Feeding areas IV and V (Bettridge *et al.* 2015; Bestley *et al.* 2019), before undertaking their annual migrations along the west and east coasts, towards their breeding grounds in the Kimberly region of Western Australia (BSD) and Great Barrier Reef Marine Park (BSE1) (Jenner *et al.* 2001; Smith *et al.* 2012). There is evidence of individuals crossing between feeding (Chittleborough 1965; Andrews-Goff *et al.* 2018) and breeding grounds (Kaufman *et al.* 2011) within these two populations, resulting in low levels of genetic differentiation between the two populations (Schmitt *et al.* 2014).

The west and east coast populations display similar migratory patterns, with whales travelling annually from Antarctic feeding areas to northern Australian breeding areas. However, their migratory route and important habitats exhibit anthropogenic and environmental differences (Commonwealth of Australia 2007, 2008, 2009). Humpback whales migrating along the west and east coasts both face anthropogenic stressors; however, stressors vary among populations. On the east coast, whales face threats from noise pollution, vessel strikes and disturbance from the heavy shipping industry, with large ports situated along the east coast and within their calving ground (Bureau of Infrastructure Transport and Regional Economics 2014; Smith *et al.* 2020). In addition, the use of permanent shark nets (gillnets) in Queensland increases the risk of entanglement for northbound- and southbound-migrating humpback whales (Bolin *et al.* 2020; Tulloch *et al.* 2020). On the west coast, whales face net entanglement threat primarily from Western Australia's largest fishing industry, the Western Rock Lobster fishery (Groom and Coughran 2012; How *et al.* 2015), and disturbances from heavy shipping traffic and tourism, including swim-with-whale tourism, in more northerly areas of their migration (Bejder *et al.* 2019; Sprogis *et al.* 2020a, 2020b). Furthermore, Australia's largest production of offshore oil and gas is situated in north Western Australia, increasing the risk of acoustic disturbance and vessel strikes on migrating whales (Geoscience Australia 2021; Thomson *et al.* 2021).

Although the west and east coasts are both flanked by warm southward-flowing boundary currents, the Leeuwin Current and the East Australian Current have different seasonal and interannual variability (Pattiaratchi and Siji 2020). This interannual variability in current strength, as well as variability induced by different phases of ENSO, is weaker along the east coast than in the west, meaning that greater differences in current strength are experienced on the west coast (Pattiaratchi and Siji 2020). The positive phase of ENSO (La Niña) and other significant climate regimes, including the Southern Annular Mode (SAM), have been linked to variation in the adiposity, diet and fatty acid profiles of BSE1 (Bengtson Nash *et al.* 2018; Groß *et al.* 2020). This significance of climatic phenomena on the diet of humpback whales (Groß *et al.* 2020) is likely to influence individual- and population-level body condition and, consequently, population growth. In addition, stable isotope values (nitrogen and carbon), used to provide insights into feeding patterns, are

different in the west and east coast populations during a positive SAM phase, indicating that the feeding grounds of these two populations may respond differently to climatic regimes and, therefore, result in different feeding opportunities (Dedden and Rogers 2022).

There have been few comparative studies between the two populations in terms of health. Those that exist have indicated that the west Australian population has comparatively lower mean lipid content, along with differing fatty acid profile and stable isotope values (Groß *et al.*, in press). In addition, the two populations may experience climate regimes in their feeding areas differently (Dedden and Rogers 2022) and employ different feeding strategies via supplemental feeding opportunities during migration (Eisenmann *et al.* 2016). However, there is a lack of empirical investigation into the difference in body condition of the two populations. The two populations are close to or fully recovered from whaling exploitation (Kent *et al.* 2012; Bejder *et al.* 2016; Noad *et al.* 2019); however, the impact and implications of the differences mentioned above may vary for the two populations, potentially affecting their continued recovery success. It is therefore imperative to provide a body condition baseline and comparison of the two populations for future and continued monitoring that will enable the identification of threats to population health and viability. This is particularly important for a sentinel species, such as humpback whales, because their nutritional health can infer the health of their feeding grounds, and help us identify changes in their environment that may influence population vital rates.

The overall aim of this study was to compare the morphology and body condition of the west and east coast humpback whale populations. More specifically, we aimed to compare the (1) morphological measurements (e.g. body width, head length, length to blowhole, width of eyes and fluke width), (2) the average body condition of each reproductive class (calves, juveniles, adults and lactating females), and (3) the change in body condition for each reproductive class over the course of the breeding season. Because of the genetic mixing between the populations, we hypothesised there would be no differences between the populations across all three aims.

## Methods

### Data collection

Data on the east coast were collected from three sites in subtropical northern New South Wales (NSW), Australia, from June to November 2020, including Ballina Head, Evans Head, and Brunswick Heads (Fig. 1). The sampling periods covered the peaks of both the northern (June–August) and southern (August–November) migrations (Russell *et al.* 2022). Migration direction was determined by time of sampling and predominate

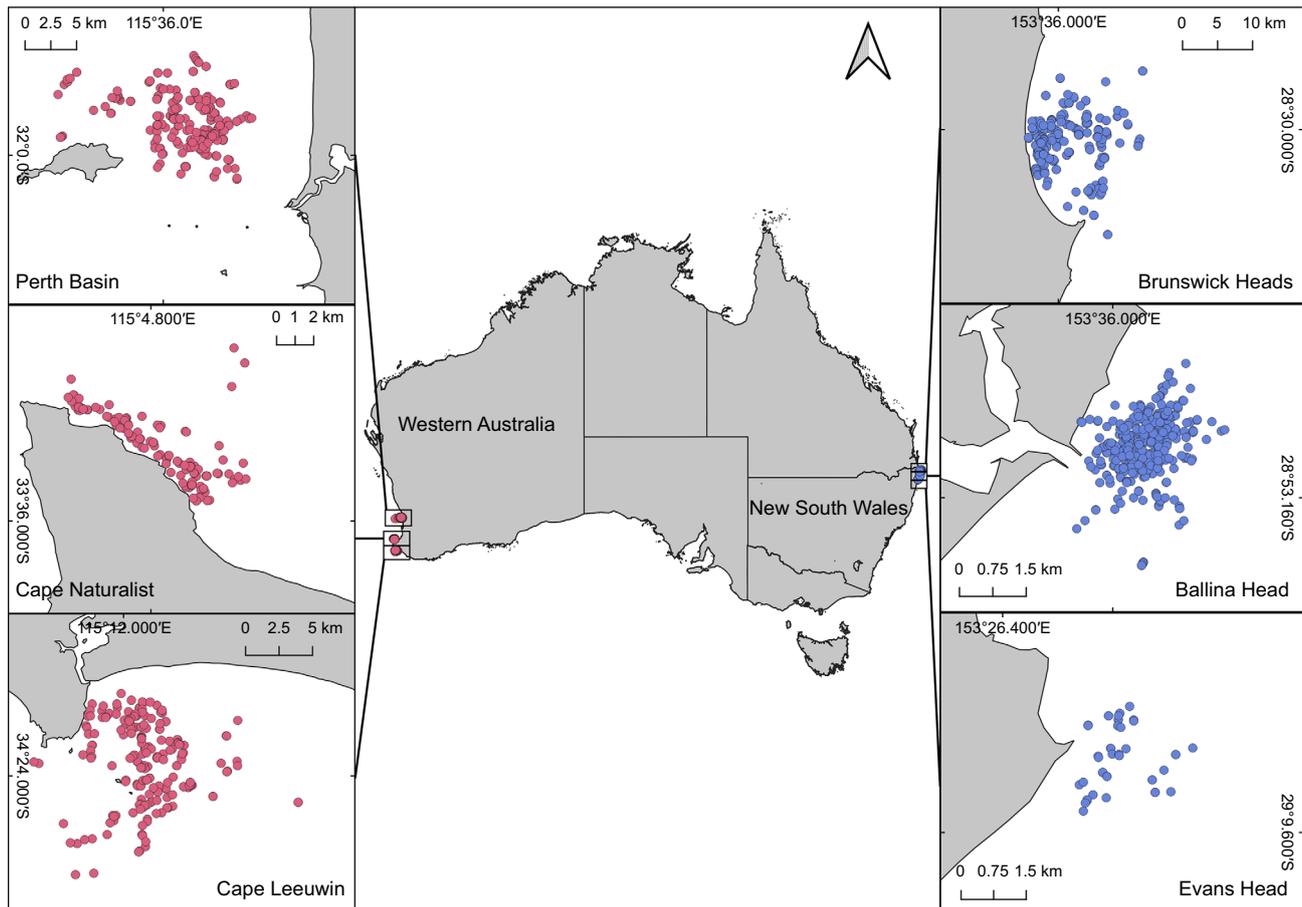
direction of travel. Data on the west coast were collected in the south of Western Australia (WA) in 2017 and 2021 from Flinders Bay (Cape Leeuwin) and Geographe Bay (Cape Naturalist), and additionally in the Perth Basin in 2021 (Christiansen *et al.* 2020b). Data for the northbound migration were obtained from Flinders Bay from April to August, and data for the southbound migration were collected from Geographe Bay and the Perth Basin between August and November (Fig. 1). The chosen locations allowed humpback whales to be sampled as they entered (northern migration) and exited (southern migration) Australian waters, to and from their breeding grounds. The study locations on Australia's west and east coasts are ~3500–4000 km from the respective feeding areas.

Along the east coast, sampling was conducted from two headland sites (Ballina Head and Evans Head) and from an 8.5 m Cougar Cat research vessel operating out of Brunswick Heads. A DJI Phantom 4 Pro UAV (weight 1388 g, diagonal size 350 mm, D1 Store Brisbane) with an integrated camera (focal length of 8.8 mm and sensor size of 12.8 × 7.2 mm) was used to record video footage of whales (Russell *et al.* 2022). The west-coast data were collected in 2021, and combined with data previously collected in 2017 (Christiansen *et al.* 2020b). In 2017, sampling was conducted from a small (~6 m) research vessel by using a DJI Inspire 1 Pro UAV (weight 3400 g, diagonal size 559 mm, D1 Store Perth) with a Zenmuse X5 camera and a 25 mm lens (sensor size of 17.3 × 13 mm), with a laser range finder attached (Christiansen *et al.* 2020b). In 2021, sampling in Western Australia took place onboard a whale-watching vessel by using the same UAV model as was used on the east coast (DJI Phantom 4 Pro).

Once a whale was sighted, the UAV was launched from either the headland (east coast) or vessel (west coast) and flown 20–60 m in altitude towards the whale. Once above the whale, the UAV descended to 20–30 m in altitude for approximately 10 min to record videos from above the whale. From this position, zenithal (from directly above) 4 K ultra-high definition (UHD) video recordings were made of the dorsal side of surfacing humpback whales. Body-height data (dorso-ventral distance) when the whale rolled on its side were also obtained to calculate body volume (from 2017 data; Christiansen *et al.* 2020b).

### Data processing

A still frame of each individual was obtained from the UAV videos. The ideal frame for photogrammetry needs the whale to be lying flat on the surface, the body straight and non-rolled, and the contours of the dorsal side clearly visible (Christiansen *et al.* 2016a). Still-frame photos of the body height were similarly extracted, with the whale rolled on the side (Christiansen *et al.* 2020b). Each still frame underwent quality control and was graded for focus, body posture, and length and width measurability, by using protocols from Christiansen *et al.* (2018).



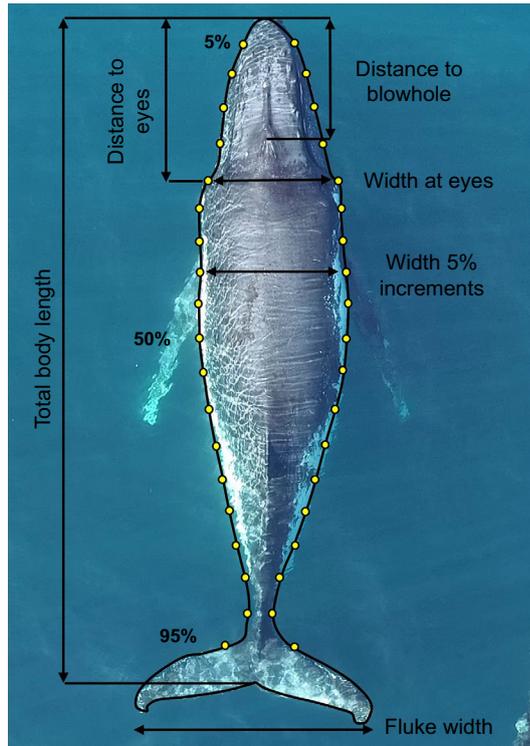
**Fig. 1.** Map of the sampling locations of the west-coast humpback whale population off south Western Australia (including Perth Basin, Cape Naturalist, and Cape Leeuwin) sampled in 2017 and 2021 and of the east-coast population off mid-eastern Australia (including Brunswick Heads, Ballina Head and Evans Head) sampled in 2020. Dots indicate the locations of all photographed individual whales, with those sampled in Western Australia in pink ( $n = 571$ ) and those on the east coast of Australia in blue ( $n = 701$ ).

Morphometric measurements, including the total body length (from the tip of the rostrum to the notch of the tail fluke), body width (at 5% intervals along the body axis), head length (from the tip of the rostrum to the eyes), length to blowhole (from the tip of the rostrum to the top point of the blowhole), and width between the eyes, were derived only for those individuals with at least a good-quality aerial photograph (Fig. 2) (Christiansen *et al.* 2016a). Body-height data were extracted using 5% intervals along the body axis, similar to body width. Using the body height of an individual will account for all body fat reserves, of which a body volume can be calculated. These measurements were completed once on each individual, by using the best still frame according to the quality-control measures. Because animals are migrating through the area, it is unlikely that the dataset contains replicates; however, to mitigate the risk of the same individual being entered into the dataset more than once, photo-identification of each individual was taken by using a DSLR camera and individuals were compared among sampling days and within a sampling day. The altitude

of the UAV (obtained from either the UAV barometric altimeter (2020 and 2021) or a laser range finder (2017)), camera sensor size, focal length and image resolution were used to convert the relative length and width measurements of the whale, expressed as the number of linear pixels in the image to absolute size (m) by using the following equation (Christiansen *et al.* 2018):

$$\text{Measurement (m)} = \left( \left( \frac{\text{Measurement pixels}}{\text{Pixels per mm}} \right) \times \left( \frac{\text{Altitude} \times 1000}{\text{Focal length}} \right) \right) / 1000 \quad (1)$$

Whales were classified according to reproductive class, including calves, juveniles, adults, or lactating females. Individuals were assigned either lactating females and calves because of the close and consistent association, and calf size being approximately <8 m in body length and/or <2/3 body length of their mothers (Sprogis *et al.* 2020a). Because historical whaling data have recorded sexual maturation of



**Fig. 2.** A photograph of a humpback whale collected via unmanned aerial vehicle, with yellow points indicating the position and black lines indicating the length of morphometric measurements, including length and width at 5% increments along the body axis to assess body condition. Body-height data were also obtained to calculate volume (see [Christiansen et al. 2020b](#)).

humpback whales to occur at approximately 11.2 m in length ([Chittleborough 1965](#)), individuals <11.2 m that were not classified as calf were classified as juveniles, whereas those  $\geq 11.2$  m were classified as adults (following [Christiansen et al. 2016a](#)).

The eastern coast data have been presented in [Russell et al. \(2022\)](#) and the west coast data have been presented in [Christiansen et al. \(2020b\)](#) and [Russell et al. \(in press\)](#). In this study, we combined the two data sets to calculate a common body condition (BC) metric for comparison. First, the body volume (BV) of the whales was calculated from the body width, body length (BL) and height data, following procedures from [Christiansen et al. \(2019\)](#). Height data were obtained using height-to-width ratios, which were calculated using still frames of whales with both dorsal (width) and lateral (height) images, from data collected during [Christiansen et al. \(2020b\)](#). Each whale was modelled using small ellipses to form the cross-section of its body at each 5% increment. The ellipses varied in the ratio of width and height according to each segment along the whale body ([Christiansen et al. 2019](#)). The volume for each body segment (ellipses) was then calculated ([Christiansen et al. 2019](#)). We used a linear interpolation of both body width

and height from 0% to 5% BL (tip of the rostrum) and from 85% to 100% BL (tail region). The total BV of a whale was calculated by the summation of all body segments and BC was calculated from the residual of the log-linear relationship between BV and BL ([Christiansen et al. 2018](#)).

### Measurement errors

The body condition metric used in this study uses the relationship between body volume (based on the body widths and heights of an individual) and the body length. Therefore, although photogrammetry studies that use UAVs carry inherent measurement errors from the recorded altitude (i.e. altimeter accuracy), the relationship between body volume and body length should remain the same. In saying this, the reported body lengths in this study will carry some error. To test the measurement error from the UAV barometric altimeter and the laser range finder used for this study, we performed calibration tests on objects of known size. Measurement errors using the laser range for the 2017 sampling year have been described in [Christiansen et al. \(2018\)](#). To test the UAV barometric altimeter for the 2020 and 2021 sampling years, two objects of 5 and 10 m were placed on a flat surface and three UAV flights were conducted over each object at altitudes of 5–100 m. Between 5 and 50 m, the UAV was flown at 5 m intervals, whereas between 50 and 100 m, the UAV was flown at 10 m intervals. A video was recorded during each flight, with a still image being extracted at each interval. At each interval, the length of the object was estimated using a custom-written script in R ([Christiansen et al. 2016a](#); [R Core Team 2021](#)) and was converted from pixels to absolute metres by using methods described in [Christiansen et al. \(2018\)](#). The percentage measurement error was calculated by comparing the estimated and actual size of the object at each altitude for each UAV flight. The measurement errors were compared at each altitude by using an ANOVA and the coefficients of variation (CV) were calculated.

### Data analysis

To investigate the differences in body-shape morphology, we used linear mixed-effects models (LME) in R v4.1.2 ([R Core Team 2021](#)). Differences in body width (as a percentage of BL) along the body axis (5–95%; width at x% body axis) of whales were compared between the east and west coasts (population) and within each reproductive class (Aim 1). As BC (and width) significantly decreases along migration direction (i.e. travelling north towards breeding grounds, compared with travelling south towards feeding grounds) ([Christiansen et al. 2020b](#); [Russell et al. 2022](#)), we used migration direction as a random variable in the model (LME: width at x% body axis ~ population (1| migration direction), subset = reproductive class). A subset of the data collected using only barometric measurements of altitude were used to compare structural morphology. We plotted each structural variable (including

head length, distance between eyes, distance to blowhole and fluke width) against body length and used generalised additive models (GAM) to test differences between the two populations (Aim 1). We used LMEs to compare the difference in mean BC between the east and west coasts (population) for each reproductive class (Aim 2) (LME:  $BC \sim \text{population}$  (1| migration direction), subset = reproductive class). Because the west coast population was sampled over 2 years, we tested the effect of year on the BC of each reproductive class in this breeding population (LME:  $BC \sim \text{year}$  (1| migration direction), subset = reproductive class). Linear models (LM) were used to investigate the change in BC over the breeding season for juveniles, adults and lactating females (Aim 3). A GAM with Gaussian family distribution was used for calves to account for non-linear relationship, because they acquire energy (from their mothers) during the breeding season. Migration time was defined as day of the year (Day) for adults and juveniles, whereas relative calf length (RCL), expressed as a percentage of the mother's body length, was used as a proxy for days post-partum for lactating females and calves (Russell et al. 2022). The BC was plotted for each reproductive class in each population against migration time (LM:  $BC \sim \text{Day/RCL}$ , subset = reproductive class and population or GAM:  $BC \sim \text{smooth spline [RCL]}$ , subset = reproductive class and population). Model selection was based on data exploration and around the energetic usage/acquisition of each reproductive class during their breeding season. Linear models and linear mixed-effects models were deemed appropriate for the temporal scale of the explanatory variable and the spread of data, whereas a generalised additive model was used for calves because their energetic acquisition may not occur linearly throughout the breeding season. Although there exists a possibility of potential biasing with regard to the timing of samples within migration direction when contrasting the two populations, there has been no discernible evidence to support migration timing influencing body condition (Russell et al. 2022). In contrast, migration direction (northbound/southbound) has been demonstrated to have a strong influence on body condition. Hence, the models accounted for migration direction by assigning a random intercept, with data assumed to be independent therein. All models were visually inspected for signs of violations of model assumptions, including homoscedasticity, normality of residuals and independence of data points. In addition, we tested the influence of outliers by using Cook's distance (Nieuwenhuis et al. 2012).

### Ethical approval

Research was conducted under a research permit from the Department of Planning, Industry and Environment (License no. SL102097), Department of Primary Industries (Permit no. MEAA20/170), Department of Biodiversity, Conservation and Attractions, WA (Permit no. 08-000702-1, and License no. FO25000334), Department of Primary Industries and Regional Development (License no. U6/2020-2022) and

animal ethics permits from Murdoch University (R2935/17 and RW3216/20) and Southern Cross University (19/052, 21/030). The UAV was operated under a UAV Operator Certificate (CASA.ReOC.0075 and CASA.ReOC.0882) as well as a Remotely Piloted Aircraft System Licence and Remote Pilot License in accordance with regulation by the Australia Civil Aviation Safety Authority.

## Results

The research effort totalled 180 survey days, with 68 days on the east coast and 112 days on the west coast (Christiansen et al. 2020b; Russell et al. 2022; Russell et al. in press). We extracted a total of 1272 still images from the UAV videos of individual humpback whales (701 on the east coast and 571 on the west coast). In total, 973 still images from individual whales passed quality control for morphometric measurements and were used in the final analysis (Table 1). There was no visible behavioural response from individual humpback whales owing to the presence of the UAV. The UAV was maintained  $\geq 20$  m in altitude, where possible acoustic disturbance from the UAV would be minimal (Christiansen et al. 2016b).

### Body length, volume and condition

The measured body lengths for individuals sampled along the east and west coasts ranged between 3.7 m and 17.10 m ( $\pm 5.3\%$  s.e.) (3.7–16.2 m on the east coast and 4.2–17.1 m on the west coast) (Supplementary Fig. S1), whereas the BC ranged from  $-0.32$  to  $0.54$  ( $-0.32$  to  $0.52$  on the east coast and  $-0.31$  to  $0.54$  on the west coast) (Table 2). The relationship between body length and body volume ( $F_{1,1008} = 3401$ ,  $P$ -values  $< 0.01$ ,  $R^2 = 0.97$ ) (Fig. 3) could be described by the equation

$$\log(BV_i) = -4.11479 + 2.96152 \times \log(BL_i) \quad (2)$$

### Measurement errors

The average measurement error using the UAV barometric altimeter to measure an object of known length was 5.3% for altitudes between 5 and 100 m. The highest errors occurred at  $\leq 15$  m, with errors of 8.8%, 10.2% and 6.9% at

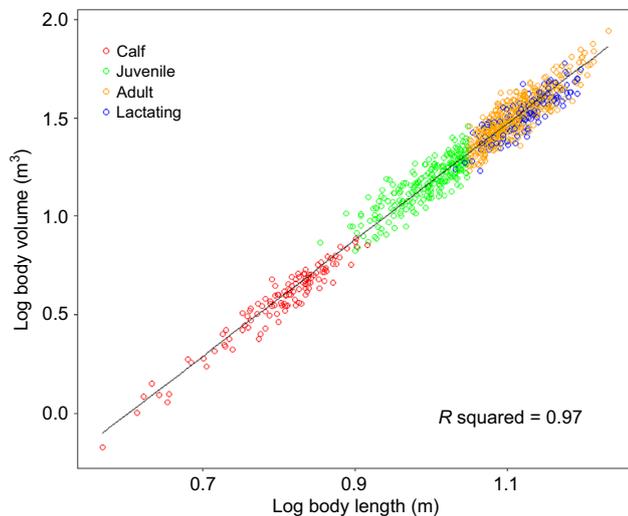
**Table 1.** Number of humpback whales of each reproductive class sampled from the east and west coasts of Australia.

Reproductive class	West coast	East coast	Total
Calves	71	48	119
Juveniles	83	166	249
Adults	235	251	486
Lactating females	71	48	119
Total	460	513	973

**Table 2.** The range, mean ( $\bar{x}$ ) and standard deviation (s.d.) of the body length and body condition for different reproductive classes of humpback whales sampled on the east and west coasts of Australia during the 2017, 2020, and 2021 migrations.

Reproductive class	Body length (m)		Body condition	
	East coast	West coast	East coast	West coast
Calf ( $\bar{x} \pm$ s.d.)	3.70–7.94 (6.00 $\pm$ 0.76)	4.19–8.47 (6.78 $\pm$ 0.81)	–0.32 to 0.34 (–0.01 $\pm$ 0.13)	–0.26 to 0.16 (–0.04 $\pm$ 0.10)
Juvenile ( $\bar{x} \pm$ s.d.)	7.95–11.2 (10.08 $\pm$ 0.83)	7.14–11.14 (9.67 $\pm$ 0.99)	–0.27 to 0.43 (0.03 $\pm$ 0.15)	–0.23 to 0.54 (0.06 $\pm$ 0.18)
Adult ( $\bar{x} \pm$ s.d.)	11.20–16.20 (12.74 $\pm$ 1.05)	11.21–17.10 (13.09 $\pm$ 1.18)	–0.23 to 0.52 (0.06 $\pm$ 0.13)	–0.31 to 0.35 (–0.02 $\pm$ 0.12)
Lactating female ( $\bar{x} \pm$ s.d.)	10.78–15.09 (12.85 $\pm$ 1.05)	11.06–16.83 (13.68 $\pm$ 1.17)	–0.20 to 0.38 (0.03 $\pm$ 0.13)	–0.28 to 0.19 (–0.10 $\pm$ 0.11)
Total	3.70–16.20	4.19–17.10	–0.32 to 0.52	–0.31 to 0.54

See Table 1 for sample sizes for each reproductive class.



**Fig. 3.** Linear model showing the relationship between the log of the estimated body length and log of estimated body volume of humpback whales (calves, juveniles, adults and lactating females) sampled on the west and east coasts of Australia in 2017, 2020 and 2021 ( $n = 973$ ).

5, 10 and 15 m respectively. There was no significant difference in measurement errors at altitudes from 20 to 100 m (Fig. S2). The average error for altitudes between 20 and 100 m was 4.48%. The lowest CV of 0.20 was recorded at 100 m altitude, whereas the highest CV of 1.26 was recorded at 5 m altitude. Owing to the significant error incurred at  $\leq 15$  m, the UAV stayed above 20 m for humpback whale measurements. The measurement error with the use of the laser range finder during the 2017 sampling year was 0.73 cm (s.d. = 0.494) (Christiansen *et al.* 2018).

### Morphometrics of the east and west coast populations (Aim 1)

Adults and lactating females showed some difference in the width of structural body areas (head and tail regions) between the two populations; however, only lactating females had a large effect size (Supplementary Table S1). Metabolically active areas along the body (25–80% BL) exhibited differences

for juveniles, adults and lactating females, whereas calves showed no difference between populations (Fig. 4, Table S1). Juveniles seemed marginally wider along the anterior section of the mid-region; however, the effect size was small (Fig. 4b, Table S1). Both adults and lactating females in the east coast population were wider across the entire metabolically active area, which is indicative of a better BC (Fig. 4c, d).

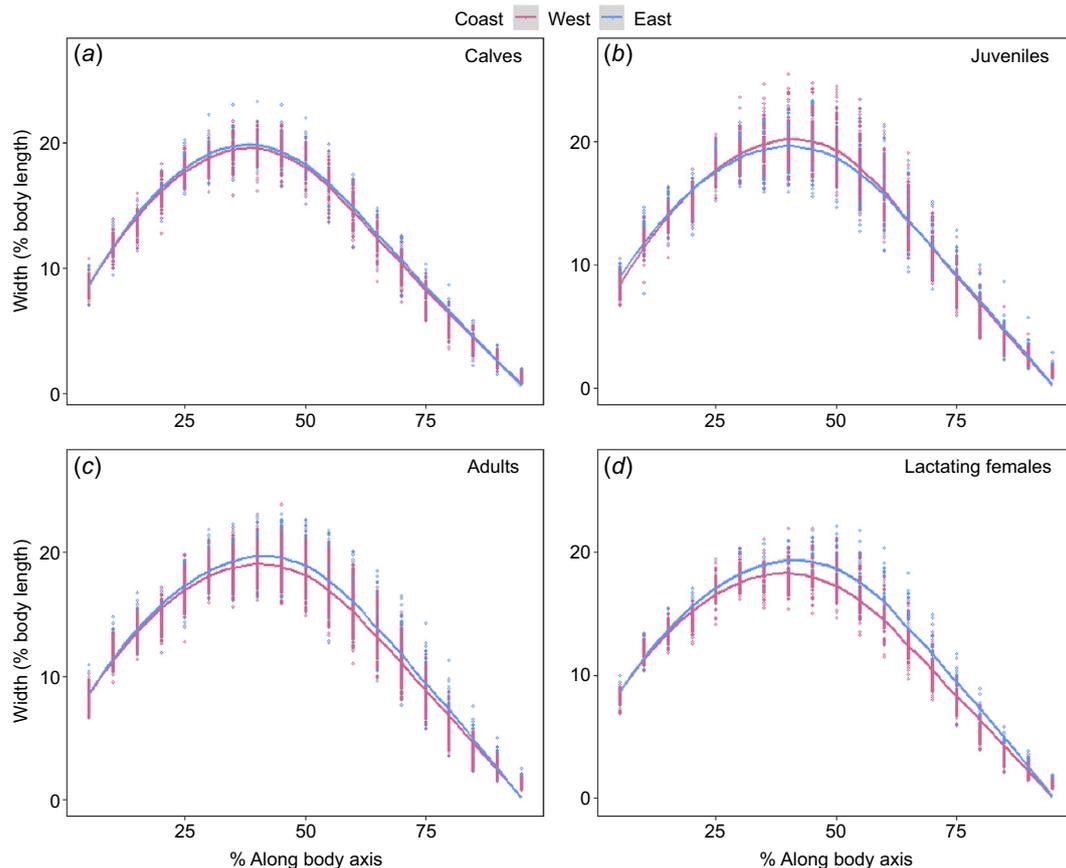
Both populations had significant ( $P < 0.001$ ) relationships with each structural variable (head length, length to blowhole, width at eyes and fluke width) and total body length (Fig. 5). However, there was no significant ( $P > 0.05$ ) difference of this relationship between the two populations for any structural variable. Only the length to blowhole differed marginally for individuals between 11 and 13 m body length, but the magnitude of difference was  $< 1\%$  (Fig. 5b).

### Body condition comparison between populations (Aim 2)

There was a significant difference between populations in mean BC for both adults ( $\chi^2 = 55.78$ ,  $P < 0.001$ ) and lactating females ( $\chi^2 = 32.46$ ,  $P < 0.001$ ) (Fig. 6). The east coast (BSE1) adults and lactating females were in a relatively better condition than were the west coast (BSD) by 7.7 and 11.1 percentage points respectively. Juveniles ( $\chi^2 = 0.44$ ,  $P = 0.502$ ) and calves ( $\chi^2 = 2.35$ ,  $P = 0.125$ ) showed no significant difference in mean BC between the two populations (Fig. 6). For the west coast population, year had a significant effect for juveniles only ( $\chi^2 = 10.54$ ,  $P < 0.01$ ) (Fig. S3).

### Change in body condition over the breeding season (Aim 3)

In both populations, all reproductive classes, with the exception of calves, showed a significant decrease in BC over the course of the breeding season. Adult humpback whales from both the east ( $F_{1,249} = 32.17$ ,  $P < 0.001$ ) and west ( $F_{1,233} = 83.44$ ,  $P < 0.001$ ) coast populations declined in BC at an average rate of 0.12 ( $\pm 0.01$ ) percentage points per day (Fig. 7a). Lactating females sampled on the east ( $F_{1,46} = 4.2$ ,  $P = 0.045$ ) and west ( $F_{1,69} = 5.15$ ,  $P = 0.026$ ) coasts showed a significant decrease in BC over the course of their migration (days post-partum), with females losing



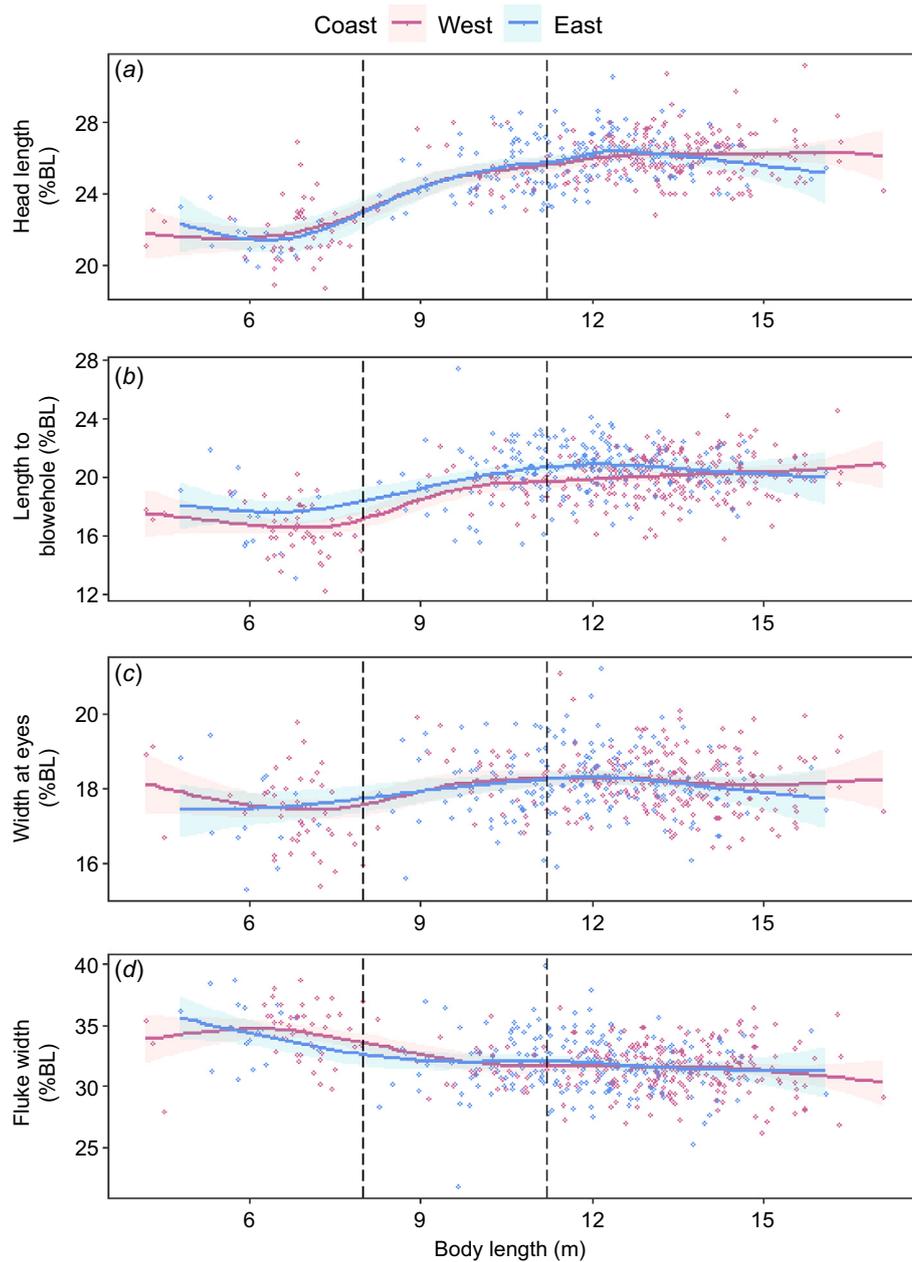
**Fig. 4.** Linear mixed-effects model showing estimated width (as a percentage of estimated body length) along the body axis at 5% increments (head to tail; 5–95%) for (a) calf (east coast,  $n = 48$ ; west coast,  $n = 71$ ), (b) juvenile (east coast,  $n = 166$ ; west coast,  $n = 83$ ), (c) adult (east coast,  $n = 251$ ; west coast,  $n = 235$ ) and (d) lactating female (east coast,  $n = 48$ ; west coast,  $n = 71$ ) humpback whales sampled on the west (pink) and east (blue) coasts of Australia. Migration direction as a random variable because width significantly decreases with migration direction (north vs south). Data points represent the width at each segment along the body axis for a particular individual.

approximately 0.60 and 0.52 ( $\pm 0.2$  s.e.) percentage points in BC with every 1% increase in calf relative length respectively (Fig. 8b). Juveniles from both the east ( $F_{1,164} = 68.61$ ,  $P < 0.001$ ) and west coasts ( $F_{1,81} = 58.26$ ,  $P < 0.001$ ) declined significantly in BC over the course of the breeding season, at a rate of 0.30 ( $\pm 0.03$  s.e.) and 0.21 ( $\pm 0.02$  s.e.) percentage points in BC per day respectively (Fig. 7b). Calves sampled on the east coast ( $F_{1,9} = 1.6$ ,  $P = 0.001$ ) showed a significant curvilinear relationship in BC change over the course of their migration (Fig. 8a), whereas calves sampled on the west coast showed no change in BC over their migration ( $F_{1,9} = 0.08$ ,  $P = 0.188$ ) (Fig. 8a).

## Discussion

This study compared the external morphology and body condition (BC) of two Australian humpback whale populations and estimated BC changes over the breeding season. The west and

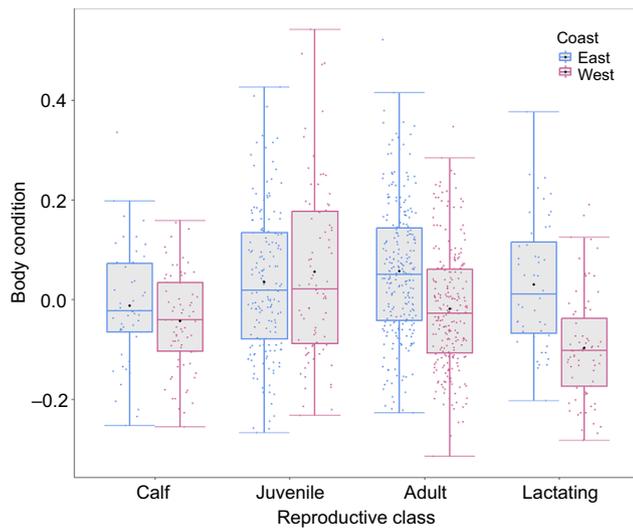
east coast populations did not differ significantly in their morphology. East coast adults and lactating females were in significantly better BC than were the west coast individuals. This could be due to differences in sampling time of each population because the west and east coast were sampled in two separate years. However, each population largely feeds, migrates and breeds in different areas, each being influenced differently by climatic regimes, climate change, and anthropogenic stressors, potentially affecting the ability of each population to acquire similar amount of energy. Both populations showed similar patterns in BC loss over the breeding season, with adults, lactating females and juveniles all declining significantly in condition over the breeding season, indicating that the energetic usage over the breeding season is similar for both populations. However, in contrast to our hypothesis, west coast calves exhibited a different relationship with migration timing (days post-partum) and BC from the east coast calves. This difference may be influenced by the poorer BC of west coast lactating females.



**Fig. 5.** Morphometric comparisons for (a) head length, (b) length to blowhole, (c) width of eyes and (d) fluke width (percentage of body length) between the east (blue) and west (pink) coast populations of humpback whales in Australia ( $n = 512$ ). Solid lines were fitted for each population by using a generalised additive model; shaded areas represent 95% confidence intervals for the model fits. The left-most dashed line represents upper limit of calf length (8 m) used in this study, and the right-most dashed line represents the body length cut-off between juvenile ( $<11.2$  m) and adult ( $\geq 11.2$  m) whales, as derived from [Christiansen et al. \(2016a\)](#).

It is worth noting that all photogrammetry studies carry inherent errors in measurement accuracy ([Christiansen et al. 2018](#); [Burnett et al. 2019](#); [Bierlich et al. 2021](#); [Ejrnæs and Sprogis 2022](#)). To test the accuracy of measurements made during this study, a calibration test was completed with six

UAV flights over an object of known length. The average error over all altitudes (5–100 m) was 5.3%, with the highest errors occurring at 5 and 10 m. No measurements of whales were taken below 20 m in altitude during this study, therefore all body length measurements presented in this study



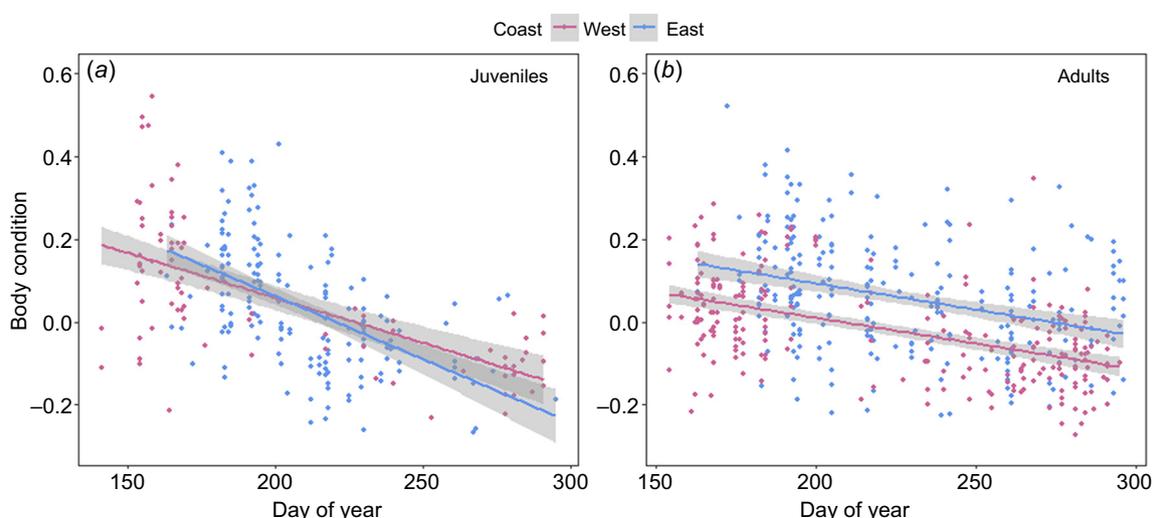
**Fig. 6.** Boxplot showing the body condition of different reproductive classes (calves:  $n = 48$  (east coast), 71 (west coast); juveniles:  $n = 166$  (east coast), 83 (west coast); adults:  $n = 251$  (east coast), 235 (west coast); and lactating females:  $n = 48$  (east coast), 71 (west coast)) of humpback whales between the west coast (outlined in pink) and east coast (outlined in blue) of Australia. Jittered points represent sampled individuals (pink = west coast, blue = east coast). The black points indicate the means for each reproductive class in their respective population. Box margins indicate upper and lower quartiles, with the solid lines representing the median body condition for each reproductive class. Whiskers depict maximum and minimum ranges of body condition.

include a confidence interval of  $\pm 5.3\%$ . Similar accuracy tests were completed by Ejmæs and Sprogis (2022), with errors of 2.1 cm ( $\sim 3\%$  for a 70 cm object) between 25 and 30 m in

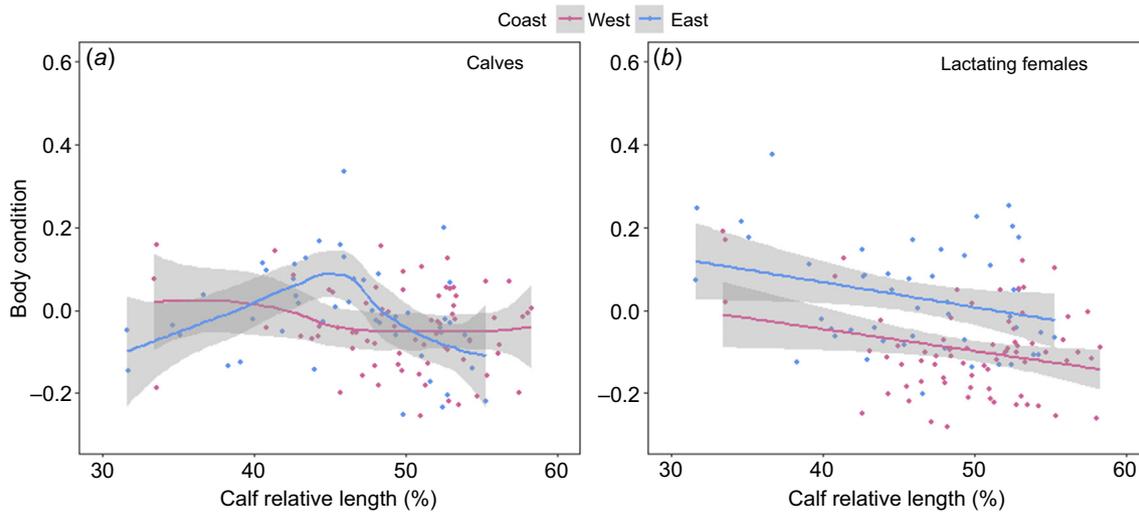
altitude, by using a Phantom 4 UAV. The largest adult in this study measured a total body length of 17.1 m, which is likely to be a measurement error. However, the method to calculate BC uses the relationship between body length and body width, so whereas length and width may carry some error, the relationship between the two variables remains the same. In saying this, there may be some precision error when measuring whales that are not completely flat, and therefore will affect the relationship used for the BC metric. Errors pertaining to this precision have been recorded at 0.30% and 0.38% for body length measurements, and 2.11% and 2.31% for body width measurement by using photographs of whales that were graded 1 or 2 for quality respectively (Christiansen et al. 2018).

### Morphometrics of east and west coast populations (Aim 1)

We did not detect morphological differences between the two populations for head length, width at eyes, or fluke width, although for individuals between 11 and 13 m in length, the distance to the blowhole was marginally longer ( $<1\%$ ) in the east coast individuals. Using historical whaling data from 1949 to 1962, Chittleborough (1965) tested the morphological difference between the two Australian populations and concluded that the difference in measurements between two observers measuring whales from the same population was greater than the difference in measurement between the two populations. The authors concluded that there may be sufficient interchange between the two populations to prevent differences in morphology and genetics occurring. In addition, morphometric measurements



**Fig. 7.** Linear models showing the change in body condition over the breeding season for humpback whales on the west (pink) and east (blue) coasts of Australia for (a) juveniles (east coast:  $n = 166$ ; west coast:  $n = 83$ ) and (b) adults (east coast:  $n = 251$ ; west coast:  $n = 235$ ). Solid lines represent predicted values from the fitted models, with 95% confidence intervals represented by grey-shaded areas.



**Fig. 8.** (a) Generalised additive model and (b) linear model showing the change in body condition with calf age (calf relative body length as a percentage of maternal body length used as a proxy for days post-partum) for humpback whale cow-calf pairs on the west (pink,  $n = 71$ ) and east (blue,  $n = 48$ ) coasts of Australia. Solid lines represent predicted values from the fitted models, with 95% confidence intervals represented by grey-shaded areas.

from humpback whales caught during whaling in two other southern hemisphere breeding populations, South Georgia (Breeding stock A, BSA) and South Africa (Breeding stock B, BSB), did not show any significant differences across the head region (Mathews 1937). Allometric growth was also considered in the studies of Mathews 1937; measurements taken from BSA and BSB found that as total length increased (i.e. with age), both populations increased the relative size of their head region and decreased the relative size of their tail region (Mathews 1937). Similar positive allometry was recorded in the present study, where relative head length and length to blowhole increased with body length, continuing to grow with length (age). The relative head length ranged between 18% and 24% of the body length when a calf, reaching between 24% and 30% of the body length when sexually mature. While length to blowhole ranged from 12% to 20% of the body length as a calf, and increased to 16–24% when sexually mature. Negative allometry was also observed, with relative fluke width decreasing with increasing body length, ranging from 30 to 40% of the body length as a calf, decreasing to 25–35% when sexually mature. This allometric growth has also been observed in other baleen whales, such as fin whales (*Balaenoptera physalus*), bowhead whales (*Balaena mysticetus*) and blue whales (*Balaenoptera musculus* sp.) (Goldbogen *et al.* 2010; Armfield *et al.* 2011; Ortega-Ortiz *et al.* 2018). When addressing the morphology of a species, it is important to consider allometric growth. One way to do this is by dividing samples into reproductive class and offering a direct comparison. The morphological and allometric results from this study, along with historical whaling data, provided evidence that the two populations are morphologically similar.

### Body condition comparison between west and east coast populations (Aim 2)

The BC estimates for west coast adults and lactating females were lower than those for the east coast by 7.7 and 11.1 percentage points respectively. This difference in BC is concerning when taking into consideration the total BC loss over an entire breeding season, when sexually mature reproductive humpback whales lose approximately 14.5 percentage points (Christiansen *et al.* 2020b). There may be several reasons as to why there is a difference in BC between the west and east coast populations, including temporal variation. Baleen whales showed fluctuations in BC among years of varying environmental conditions (Lockyer 1986; Vikingsson *et al.* 2013; Soledade Lemos *et al.* 2020; Wachtendonk *et al.* 2022), with the potential for this change to be extreme (Coughran *et al.* 2023). This may lead to different amounts of acquired energy among different feeding seasons and, in turn, a poorer or better BC at the time of sampling. Climate drivers, including the El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM), affect environmental conditions and resource availability in the Southern Ocean (Stammerjohn *et al.* 2008; Holland *et al.* 2017; Fogt and Marshall 2020), which can, in turn, affect the nutritional condition of predators. In particular, changes to sea ice in Antarctica can result in dramatic changes in the abundance of lower trophic organisms that rely on such habitats for food sources and survival. For example, Antarctic krill (*Euphausia superba*), which is a species of primary prey for humpback whales, is highly sensitive to changes in ocean conditions as it relies on sea-ice extent during larval and juvenile stages of life (Loeb *et al.* 1997; Nicol 2006).

A decrease in sea-ice extent owing to ENSO or the SAM will likely cause a change in krill larval recruitment and survival (Loeb *et al.* 1997; Quetin *et al.* 2007), and also prey availability for top Antarctic marine predators such as humpback whales (Flores *et al.* 2012), and in turn affect the amount of energy acquired during a feeding season (Pallin *et al.* 2023). The feeding season prior to data collection for the east coast took place during the austral summer of 2019–20, during a neutral ENSO phase (Bureau of Meteorology 2022), whereas the feeding seasons prior to data collection for the west coast were the austral summers of 2016–17 and 2020–21, during a La Niña watch and La Niña active (moderate to strong level) respectively. During these times, the SAM was predominantly in a positive phase, with negative phases occurring briefly at the end of 2017 and 2019 (NOAA 2023).

Humpback whales are an important sentinel species, meaning that they are reliable indicators of oceanic ecosystem health and environmental change (Bengtson Nash *et al.* 2018). Quantifying biological processes of these sentinel species, such as condition and diet, and how they respond to environmental changes or fluctuating prey availability, is an important step in understanding how climatic regimes or climate change may affect these populations. A study examining the adiposity and diet of the east coast humpback whales over an 8-year period found that a particularly lean year in terms of adiposity for the population (2011) coincided with one of the strongest La Niña events on record (Bengtson Nash *et al.* 2018). In addition, elevated concentrations of nitrogen and carbon stable isotopes were found in the baleen plates of east coast humpback whales corresponding to La Niña events, potentially indicating reduced feeding opportunities during La Niña (Dedden and Rogers 2022). Furthermore, 23% of the variation in fatty acid profiles (used to indicate dietary consumption) in eastern coast whales was explained by SAM, indicating the significance of these climatic phenomena on the diet of humpback whales (Groß *et al.* 2020). On the basis of this, it is possible that the conditions resulting from La Niña and the positive SAM negatively affected the BC during the feeding season of the west coast population, resulting in a poorer BC for adults and lactating females than for the east coast population.

Estimated calf BC was similar between the two populations, despite the BC of lactating females being significantly poorer in the west coast population. Humpback whales exhibit a positive linear relationship between maternal and calf BC, whereby fatter mothers generally have fatter calves (Christiansen *et al.* 2016a). This is because the energy reserves a female carries will determine fetal growth rates, birth size, and calf growth rates (Christiansen *et al.* 2018, 2022), which should aid their swimming ability and survival. Therefore, because the estimated BC of lactating females was significantly poorer in the west coast population, one would expect west coast calves to also display poorer BC than that of the calves in the east; however, this was not the case. Our results are similar to those reported for North Atlantic

right whale mothers, which showed significantly poorer BC than did the southern right whale mothers, whereas their calves exhibited a robust BC (Christiansen *et al.* 2020a). The mean growth rate of the North Atlantic right whales has decreased since 1981 (Stewart *et al.* 2021), which may reflect decreasing BC in mothers (Christiansen *et al.* 2020a). Consequently, North Atlantic right whales are potentially extending their weaning time, which may be causing longer inter-calving intervals (Christiansen *et al.* 2020a). Future investigations examining reproductive intervals in the two Australian humpback populations could provide further insight and determine whether the west coast populations exhibit extended weaning and longer inter-calving intervals as a result of poorer overall BC. If this is the case, we would expect to see population growth decrease from the previously reported rate of 13% in 2012 (Kent *et al.* 2012), making continued monitoring important for this population, so as to identify any decline in body condition from the baseline reported in this study.

### **Body condition change over the breeding season and comparison between populations (Aim 3)**

Capital breeding baleen whales store energy in the form of blubber, muscle and visceral fat (Lockyer 1987). Variation in this stored energy can be observed by physical changes (i.e. fattening and thinning) in their body volume because of the seasonal feeding/fasting strategy (Lockyer 1987; Niæss *et al.* 1998; Christiansen *et al.* 2020b). All reproductive classes, with the exception of calves, followed a similar pattern of BC change over the breeding season. Our results showed that sexually mature individuals from the west coast arrived in Australian waters in poorer BC than did those in the east coast population, but maintained a similar difference in BC throughout their migration. This indicates that the differences observed during this study are most likely to be due to differences in energetic acquisition over the feeding season rather than differences in energetic usage over the breeding season. Both adult and lactating female humpback whales decreased BC over their breeding season (Christiansen *et al.* 2016a, 2020b; Russell *et al.* 2022). Our results indicated that this decline in condition happens at a similar rate for both populations. Juveniles exhibited no difference in BC between populations, arriving and departing Australian waters in relatively similar conditions, and declining in condition at a similar rate throughout the breeding season. This was not the case in Exmouth, Western Australia, where juveniles maintained their BC; however, data were taken closer to the breeding grounds and therefore may not reflect the full BC change over the breeding season (Christiansen *et al.* 2016a). Contrary to this, calves displayed different BC change over the breeding season between the two populations. We expected calves to increase in BC throughout the breeding season because they are nursing on high caloric milk from their mothers (Oftedal 1997). However, calves from the western

coast maintained their BC, rather than increasing their BC, a similar pattern to that from Exmouth population (Christiansen *et al.* 2016a). However, calves from the east coast exhibited a curvilinear relationship over the breeding season, with early and late-migrating calves being in a significantly poorer BC than those migrating mid-migration (40–50% mother's body length). The poorer condition of mothers from the west coast may be a contributing factor to differences in BC change of their calves over the breeding season. In addition, factors that this study did not test, including milk richness, behavioural differences or anthropogenic disturbances (i.e. boater presence) disrupting nursing, could cause differences observed in this study.

## Conclusions

This study compared the morphology, BC and energetic usage over the breeding season of the two populations of humpback whales that migrate to northern Australian breeding grounds. We estimated a poorer BC in sexually mature individuals from the west coast than in those from the east coast, which is concerning given the BC difference is comparable to the BC loss during a full breeding season where individuals are predominantly fasting for 4–5 months. Although the direct consequences of this BC difference are not known, it is speculated that a poor condition may contribute to extended weaning time and longer inter-calving intervals (Christiansen *et al.* 2020a). The difference shown in this study could be influenced by variations in sampling time; however, differences in feeding opportunities, climatic regimes and/or environmental variables may also influence nutritional condition. These two populations, according to the latest estimates, are growing in abundance and are considered to be the two largest breeding populations in the world (Fleming and Jackson 2011; Kent *et al.* 2012; Noad *et al.* 2019). The few comparative studies between the two populations have shown that they experience climate regimes differently (Dedden and Rogers 2022), and also differ in feeding strategies (Eisenmann *et al.* 2016) and the associated mean lipid content (Groß *et al.* in press). These differences may influence their respective ability to sustain the high population levels that have been reported for these two populations, when subject to severe anthropogenic disturbances or reduced prey availability owing to climate-induced environmental changes (Kent *et al.* 2012; Noad *et al.* 2019). In addition, the migratory routes for each population exhibit variation in both anthropogenic stressors and environmental variables. With this in mind, it is important to provide separate baseline information on the BC of each population, so as to develop custom management plans that take into account the unique variables, threats and current condition of each population. Although the Australian humpback whale populations were recently delisted from the Endangered Species List (DAWE 2022), regular monitoring of

their BC (every 5 years) is recommended to ensure that the population remains healthy. In addition, regular monitoring of a sentinel species, such as humpback whales, will help us understand changes in their Southern Ocean feeding grounds and how climatic phenomena influence the health and vital rates of each population.

## Supplementary material

Supplementary material is available [online](#).

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**Data availability.** The data that support this study will be shared upon reasonable request to the corresponding author.

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#### Author affiliations

<sup>A</sup>Marine Ecology Research Centre, Southern Cross University, Military Road, East Lismore, NSW 2480, Australia.

<sup>B</sup>Department of Ecoscience, Marine Mammal Research, Aarhus University, Roskilde 4000, Denmark.

<sup>C</sup>Sci-eye, PO Box 4202, Goonellabah, NSW 2480, Australia.

<sup>D</sup>The Oceans Institute and School of Biological Sciences, The University of Western Australia, Albany, WA 6330, Australia.