Conservation Physiology

Volume 14 • 2026 10.1093/conphys/coag093

SEB SOCIETY FOR EXPERIMENTAL BIOLOGY

Research article

# A novel comparison of live whale body condition assessment methods from lateral images with necropsy-derived metrics and histology in gray whales (*Eschrichtius robustus*)

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Body condition (BC) is a critical indicator of health, reproductive viability and ecosystem capacity in cetaceans. Validating BC assessment methods from live animals against direct physiological measurements remains challenging, particularly in large whales. BC of live grey whales (*Eschrichtius robustus*) is commonly assessed from lateral imagery by categorical scoring systems, although these have not been directly compared to necropsy-derived metrics. We evaluated two live whale lateral BC assessment methods, the Bradford scoring system and the recently developed angle of BC (°BC), using photographs of live grey whales in San Francisco Bay that were subsequently matched to stranded carcasses. Inter-rater reliability was high for both methods, and results were correlated as expected. We then compared each live BC assessment method to necropsy-derived metrics including blubber depth, qualitative blubber characteristics, state of nutrition (SON) and adipocyte histology at three blubber levels: deep, middle and superficial. Neither °BC nor Bradford score was significantly associated with blubber thickness or characteristics, suggesting that blubber depth is an unreliable proxy for nutritional condition. Notably, °BC significantly predicted SON while Bradford scores showed weaker and non-significant relationships with SON. Adipocytes in the deep blubber layer were depleted and therefore not assessable. Furthermore, °BC significantly predicted adipocyte morphology of the middle blubber layer but not the superficial layer, and the deep layer was too depleted for assessment. Contrastingly, Bradford scores did not predict adipocyte morphology at any layer. These findings provide the first direct comparison of live large whale BC assessment against necropsy-derived metrics in the same individuals, supporting the use of quantitative lateral-image analysis as a sensitive non-invasive tool for assessing grey whale health. Additionally, the significance of °BC as a predictor of adipocyte morphology indicates that nutritional status can be reasonably inferred from blubber histology with limited imagery or samples available.

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### Lay Summary

Monitoring whale health and body condition is essential for conservation, but accurately assessing living whales remains difficult. By comparing photographs of whales with subsequent necropsy findings, we found an association between a quantitative measure and both histology and necropsy findings. This measure outperformed traditional scoring, reflecting necropsy assessed nutritional status.



**Key words**: Adipocyte, blubber depth, body condition, health, histology, method validation, necropsy, physiology


**Abbreviations:** BC, body condition; CI, confidence interval; ICC, intraclass correlation coefficient; LRT, likelihood ratio test; NOAA, National Oceanographic and Atmospheric Administration; OR, odds ratios; PCH, post-cranial hump; SE, standard error; SF Bay, San Francisco Bay; SON, state of nutrition; TMMC, The Marine Mammal Center; UAS, unmanned aircraft system


**Editor:** Andrea Fuller

Received 22 July 2026; accepted 2 November 2026

**Cite as:** Slaathaug JM, Duignan PJ, Telford KA, Flannery M, Wilkin AM, Grimes A, Lane RS, Halaska B, Calambokidis J, Crocker DE (2026) A novel comparison of live whale body condition assessment methods from lateral images with necropsy-derived metrics and histology in gray whales (*Eschrichtius robustus*). *Conserv Physiol* 14(1): coag093; doi:10.1093/conphys/coag093.


## Introduction

Understanding population health is central to revealing how ecosystem processes shape species dynamics and survivorship. Long-term monitoring of population health provides crucial baseline information necessary to detect and evaluate the impact of unusual mortality events, ecosystem disturbances and other long-term environmental perturbations, including those associated with climate change (Gagnon *et al*., 2011; Williams *et al*., 2013; Rolland *et al*., 2016; Castrillon & Nash, 2020; Kucklick *et al*., 2022; Lindenmayer *et al*., 2022; Stephen, 2022; Eguchi *et al*., 2025). Body condition (BC), defined as the relative size of an animal's energy reserves, is a valuable proxy of individual health directly linked to fitness and reproductive success in many species (Lockyer & Waters, 1986; Sæther, 1997; Stevenson & Woods, 2006; Schamber *et al*., 2009; Miller & Hall, 2012; Williams *et al*., 2013; Christiansen *et al*., 2014; van Aswegen *et al*., 2024; Pirotta *et al*., 2025). BC is also strongly associated with prey availability and therefore serves as an indicator of the capacity of an ecosystem to sustain the members of its population (Sæther, 1997; Reading, 2004; Stevenson & Woods, 2006; Øigård *et al*., 2013; Williams *et al*., 2013; Harwood *et al*., 2015; Stewart *et al*., 2021). Examining BC of individuals has served as a valuable tool for understanding ecosystem and population health on broad scales.

Assessing BC in living cetaceans can be challenging due to several constraints, including limited visibility of the body while surfacing and the evasive nature of some species (Castrillon & Nash, 2020). In small odontocetes, BC and other health metrics are completed frequently on wild-captured animals that are later released (Ridgway & Fenner, 1982; Hart *et al*., 2013; Joblon *et al*., 2014; Castrillon & Nash, 2020; Cicciarella *et al*., 2026). In large whales, the inability to capture and handle animals amplifies the challenge of measuring BC accurately, and many studies have relied on animals killed for whaling or otherwise stranded (Rice *et al*., 1971; Lockyer & Waters, 1986; Christiansen *et al*., 2020; Raverty *et al*., 2020, 2024). Physical health examinations of large whales have been rare throughout history and are limited to a few animals taken in for rehabilitation or examined in the wild, many for the purpose of cardiovascular research (Senft & Kanwisher, 1960; Curran & Asher, 1974; Meijler *et al*., 1992; Reidarson *et al*., 2001; Miller *et al*., 2011). To circumvent the challenges of live large whale BC measurement, non-invasive or minimally invasive techniques such as biopsy dart sampling, aerial photogrammetry from unmanned aircraft systems (UASs; drone) or aerial surveys, and methods for assessing lateral photographs have been developed and widely used (Perryman & Lynn, 2002; Pettis *et al*., 2004; Bradford *et al*., 2012; Kershaw *et al*., 2019; Castrillon & Nash, 2020; Soledade Lemos *et al*., 2020; Moore *et al*., 2021). As UAS technology improves and becomes more accessible, photogrammetry from UAS-derived images is generally considered the most accurate technique for use with large, free-swimming whales (Christiansen *et al*., 2016; Burnett *et al*., 2019; Castrillon & Nash, 2020; Cicciarella *et al*., 2026). However, many institutions have an archive of lateral photographs from historical photo-identification datasets that can be used to provide valuable temporal benchmarking or retrospective information, and lateral image analysis can be used to evaluate free-swimming animals in areas with limited resources or permitting restrictions to conduct UAS operations (Pettis *et al*., 2004; Gendron *et al*., 2015; Castrillon & Nash, 2020).

Methodologies for determining BC from lateral photographs are well-established and used in several cetaceans species including grey whales (*Eschrichtius robustus*), blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), Indo-Pacific humpback dolphins (*Sousa chinensis*) and North Atlantic right whales (*Eubalaena glacialis*) (Pettis *et al*., 2004; Bradford *et al*., 2012; Wachtendonk *et al*., 2022; Boileau *et al*., 2024; Serres *et al*., 2026). These methods primarily rely on lateral images taken of either the animal's cranial or cervical region, and for some species the dorsal flank. In grey whales,

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the cranial and cervical regions have been demonstrated to be the most informative (Bradford *et al*., 2012). The extent of subcutaneous fat storage on each whale alters its appearance, and as the fat storage in the nuchal crest depletes, a cervical indentation or post-cranial depression, commonly known as a 'peanut head', becomes evident and the scapula may become more prominent (Curran & Asher, 1974; Pettis *et al*., 2004; Raverty *et al*., 2020). In grey whales, the primary assessment of live whale BC from lateral photographs has been a scoring system known as the Bradford method, which results in a whale being scored as poor (one), fair (two) or good (three) (Bradford *et al*., 2012). This method relies on trained observers to visually assess lateral photographs of a whale, examine the appearance of the post-cranial, scapular and flank areas, and assign them a score based on the presence and prominence of indentations corresponding to the absence of subcutaneous fat. A whale in poor condition would have a post-cranial depression, post-cranial hump (PCH), prominent scapula and a divot along the flank all indicating fat loss. A whale in fair condition may have some but not all of these features, and a whale in good condition would have the rounded contours of an animal with sufficient body fat to mask skeletal structures beneath.

Recently, an alternative method for assessing lateral images of grey whales was developed with the goal of generating more fine-scale data from historic datasets and assessing individual fat gain using an angle of BC (°BC) measurement (Telford *et al*., 2026). This angle measurement quantifies the depth of the post-cranial depression, allowing the severity of fat depletion to be quantified beyond a categorical score or simple presence/absence of the feature. This method has only been previously described and deployed in its development study on a small, annually returning group of grey whales in Puget Sound. Within the developmental study, preliminary data from both lateral image analysis (°BC) and UAS-derived BC index demonstrated agreement between methodologies and the need for further validation of each throughout the species range (Telford *et al*., 2026).

Necropsies are widely regarded as the gold standard in evaluating an individual's health, since they allow direct physical measurements and sampling for a wide array of examination types including histology (Wilder *et al*., 2016; Zhang *et al*., 2023; IJsseldijk *et al*., 2024; Lennon *et al*., 2025). In most cases, these direct examinations provide data beyond what an animal may present while alive, and give insight into several health metrics beyond cause of death (Lennon *et al*., 2025). Necropsy studies have developed a methodology for determining the BC of an animal, taking into account factors such as external body contour, fat appearance and storage in the blubber (thickness and consistency), subcutaneous fat deposits (such as the nuchal fat pad) and cavitary fat present in membranes (pleural, pericardial, mediastinal, peritoneal and mesenteric) or on the capsule/serosa of organs (e.g. renal fat) (Niæss *et al*., 1998; Koopman *et al*., 2002; Williams *et al*., 2013; Raverty *et al*., 2020, 2024). In grey whales, an index was developed specifically to guide determination of BC post-mortem, incorporating all data available on the animal and establishing a state of nutrition (SON) ranking, also referred to as nutritional condition (Raverty *et al*., 2024). A limitation of necropsy studies, however, is that stranded animals may represent a biased sample of the overall population including the very young, very old or otherwise compromised (Christiansen *et al*., 2020; Lennon *et al*., 2025). Additional limitations include decomposition, bloating and logistical challenges such as location of the carcass, tide cycles and daylight limiting access or carcass recumbency preventing full examination of the dorsum. Reliable determination of BC also relies on dedicated observers, responders and pathologists, which has proven challenging for retrospective studies (Raverty *et al*., 2020).

Blubber histology including assessment of adipocyte morphology (shape, size and contour) and total lipid content from both live and dead cetaceans have often been utilized to infer BC (Koopman *et al*., 2002; Evans *et al*., 2003; Waugh *et al*., 2012; Castrillon *et al*., 2017; Druskat *et al*., 2019; Castrillon & Nash, 2020). Blubber is stratified into three layers, with the innermost (or deep) layer understood to be the most metabolically active, while the outermost (or superficial) layer is critically important for maintaining hydrodynamic shape and thermoregulation (Lockyer & Waters,1986; Aguilar & Borrell, 1990; Koopman *et al*., 2002; Struntz *et al*., 2004; Strandberg *et al*., 2008; Castrillon & Nash, 2020). This stratification provides a challenge when assessing BC from live whale biopsy samples, as studies have shown little to no association between lipid concentration in the sampled superficial layer with BC measurements derived from aerial photographs or lateral images (Evans *et al*., 2003; Kershaw *et al*., 2019; Christiansen *et al*., 2020; Magallon Flores *et al*., 2024). Additionally, total lipid content and/or adipocyte assessment is not correlated with blubber thickness across species (Evans *et al*., 2003; Gómez-Campos *et al*., 2011; Kershaw *et al*., 2019; Castrillon & Nash, 2020). Blubber histology is considered to be an improved approximation of BC compared to blubber thickness, although histology images are evaluated in a variety of ways including manual review and automation (Castrillon & Nash, 2020).

A review of published BC methodologies by Castrillon and Nash (2020) described the ideal criteria for a BC metric as (i) sensitive, (ii) nonlethal, (iii) inexpensive and (iv) versatile and applicable to categories such as both alive and dead animals (Castrillon & Nash, 2020). While a few live-to-live methodology comparisons have been conducted, results have been variable (Bengston Nash *et al*., 2013; Christiansen *et al*., 2020; Aoki *et al*., 2021). It is extremely rare, however, that BC assessment methods for live whales are validated or compared to necropsy results for the same individuals. Comparison of methodologies is critical to assess validity and alignment of approaches and ensure that the same conclusions are drawn about the health of an individual regardless of methodology used (Schamber *et al*., 2009; Castrillon & Nash, 2020; Telford *et al*., 2026). Validation of live BC techniques to physical measurements has been identified as a critical need in previous research across many species of cetaceans (Curran & Asher, 1974; Evans *et al*., 2003; Stevenson & Woods, 2006; Hart *et al*., 2013; Williams *et al*., 2013; Wilder *et al*., 2016; Kershaw *et al*., 2017, 2019; Castrillon & Nash, 2020; Christiansen *et al*., 2020; Raverty *et al*., 2020; Larrat & Lair, 2022; Cicciarella *et al*., 2026). The opportunity to make these comparisons is especially rare in large whales, however, as many carcasses are not recovered and the rapid loss of skin during decomposition makes matching to photo-identification catalogues difficult (Moore *et al*., 2020; Slaathaug *et al*., 2026).

Studies that have matched live whales to their carcasses with a completed necropsy add critical context to the data collected both while the individual was alive and post-mortem during necropsy or

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sampling (Lowe *et al*., 2021; McGuire *et al*., 2021; Slaathaug *et al*., 2026). In San Francisco Bay (SF Bay), California, the recent influx and mortality of grey whales in an urban setting provided a valuable opportunity to match carcasses with live individuals (Slaathaug *et al*., 2026). SF Bay is located nearly halfway along the population's extensive migratory route and has been hypothesized to be an emerging feeding ground during a time of overall nutritional stress and pressure in the population (Slaathaug *et al*., 2026). In this study, we utilized photographs of live grey whales matched to stranded carcasses in SF Bay to compare two lateral-image BC assessment methods to necropsy-derived metrics and histology. To the best of our knowledge, this is the first comparison of live whale methodology to direct measurements from necropsy in baleen whales.

# Materials and Methods

## Data collection

Sightings information and associated photographs of grey whales in SF Bay were collected by The Marine Mammal Center (TMMC) from 2018 to 2025 from a variety of sources including dedicated research surveys (NOAA-NMFS Permit #26532), community reports, and naturalist submissions. The resulting photo-identification catalogue of 115 grey whales was compared to photographs of carcasses from the same time frame, resulting in 21 matched individuals (Slaathaug *et al*., 2026). We then examined the historic, opportunistic photographic database for suitable images for BC assessment for the last known live sighting of each of the 21 matched whales.

Image quality was considered paramount with high-resolution DSLR images prioritized to allow for more accurate measurements (Telford *et al*., 2026). The lowest quality image included was 1334 × 2672 pixels and the majority of the images were over 3000 × 5000 pixels. Suitable images were those in which the whale was: (i) perpendicular to the camera in focus, (ii) with little to no glare present on the water, (iii) in which the blowhole, post-cranial area and part of the back or flank were visible and (iv) with the whale parallel to the surface of the water and with little to no dive pitch. The distance from the photographer to the whale was considered, and images were excluded if the whale's body did not span at least 20% of the overall pixel width, all over 1200 pixels. If there were no images of acceptable quality on the last sighting, each sighting prior was examined until one was identified. All whale necropsies and sampling were conducted under authorization by the National Oceanographic and Atmospheric Administration (NOAA), National Marine Fisheries Service through Stranding Agreements issued to the California Academy of Sciences and TMMC (Slaathaug *et al*., 2026).

## Live whale body condition assessment

To assess live whale BC, we employed and compared the Bradford methodology and °BC on photographs of the post-cranial areas only. Using the Bradford method, reviewers assign ordinal scores of one to three (poor to good) to each image based on the appearance of the body shape indicating fat loss, whereas the °BC method is a calculated angle measurement of the severity of cervical fat loss resulting in a post-cranial depression (Bradford *et al*., 2012; Telford *et al*., 2026). For objectivity, two trained reviewers employed both methods independently and double-blinded to whale identity and results from the other assessor. Authors A.M.W. and J.M.S. assigned images a Bradford score, while authors J.M.S. and K.A.T. measured each image's °BC.

To assign a whale a BC score using the Bradford methodology, the post-cranial area was examined closely for nuchal fat loss indicated by the presence of a pronounced hump, a divot, or both. Bradford scoring in the post-cranial area is classified as either one (poor), presence of both a pronounced hump and a divot; two (fair), presence of a divot but not hump; or three (good), no divot or hump present (Bradford *et al*., 2012). To assess inter-rater reliability, a weighted Cohen's Kappa (κ) was calculated (Cohen, 1968; Wright *et al*., 2011). Although Bradford's method can produce a BC score from photographs that do not include the post-cranial area, for the purposes of this study we chose to use only post-cranial images as to retain conformity with the °BC method.

To determine a whale's °BC, the line and angle tools on the open-source photo-editing software ImageJ were used (Schneider *et al*., 2012; Telford *et al*., 2026). The line tool is first used to determine the length ($L$) from the top of the blowhole to the top of the PCH (Fig. 1, panel A). $L$ is then duplicated to denote an anchor point along the whale's back posterior to the blowhole (Fig. 1, panel B). °BC is subsequently calculated as the lowest point of the body shape or cervical depression between these two anchor points, the top of the PCH and the back point anchor (Fig. 1). This yields a data record of $2L$ and an angle measurement (°BC). The lower the °BC, the better condition that the whale is in, reflecting a minimal depression. Though negative measurements were found in the initial development of the method, in this study no whales were found to have an °BC below zero (Telford *et al*., 2026). Inter-rater reliability for these measurements was assessed using a two-way absolute-agreement intraclass correlation coefficient (ICC[2,1]) for single measurements, with greater ICC values indicating greater agreement in °BC between raters and therefore greater measurement reproducibility (Koo & Li, 2016). To evaluate whether one rater systematically scored higher or lower than the other, a paired $t$-test was performed comparing the two raters' °BC measurements for the same whales.

## Necropsy body condition assessment

The level of necropsy, examination, and sampling conducted among the individuals in this study varied considerably. Carcass recumbency, position, and location can limit metrics assessed on each individual. NOAA's large whale necropsy form was reviewed for each case and all data from the necropsies used in this study were transcribed from them. After necropsy, this form is completed by the lead pathologist or participant present at time of necropsy and consistently reviewed by the pathology department. The decomposition state of the carcass was classified at necropsy as alive, fresh dead, moderate decomposition, advanced decomposition, skeletal/mummified remains or undetermined using the Decomposition Condition Code based on post-mortem changes (Geraci & Lounsbury, 1993). One individual included in this study was considered in advanced decomposition state, while the rest were fresh to moderately decomposed. Only a skin and blubber sample was collected from the carcass in an advanced state

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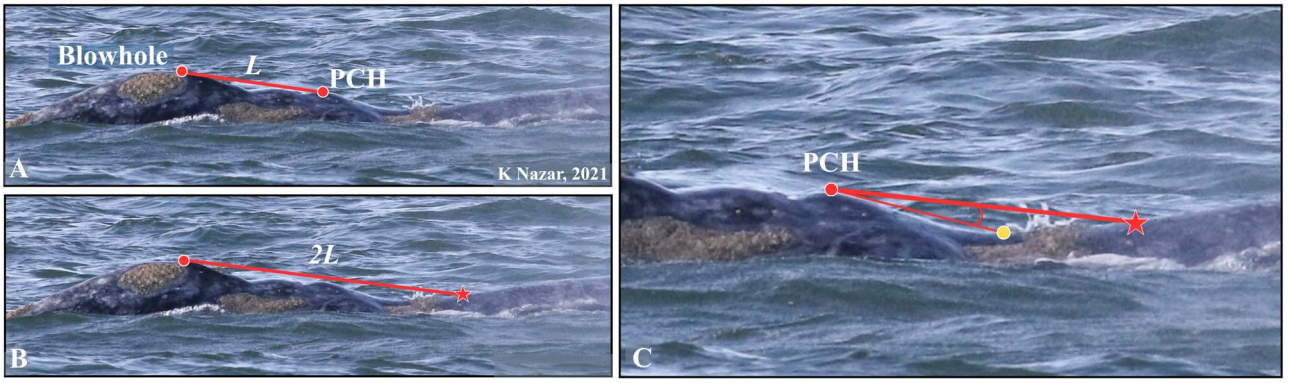



**Figure 1:** The °BC measurement process. Panel a shows the °BC measurement process of *L*, and panel B follows showing 2*L* with the flank anchor point shown as a star. Panel C shows the process of creating the angle measurement between the PCH and the lowest point of the cervical depression (middle dot).

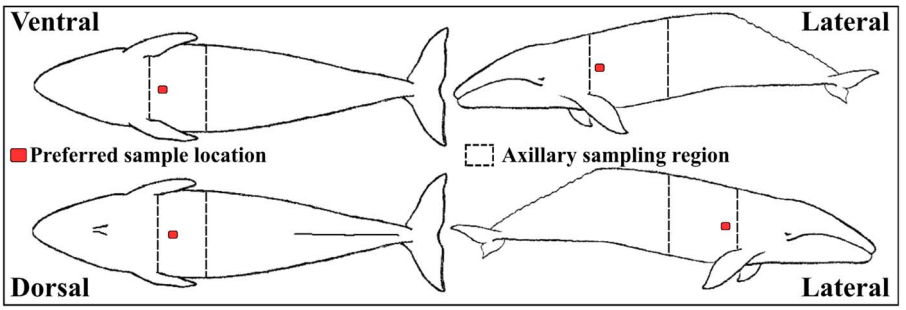



**Figure 2:** Adapted from NOAA's large whale necropsy form; the axillary region for blubber sampling on grey whales is shown in the dashed black line, and the solid box shows the preferred location for sampling.

of decomposition, as it was entrapped underneath the pilings of an oil refinery.

The necropsy-derived metrics of BC examined in this study were blubber oil content, blubber fibre description and blubber depth measurements from three areas of the circumference (mid-dorsal, mid-lateral and mid-ventral) at the level of the axilla (Fig. 2). The full thickness of the blubber depth was measured from the base of the epidermis to the subcutaneous connective tissue, though it is important to note the recumbency of carcasses proves challenging for standardizing the exact location of a blubber depth measurement.

Blubber oil content was subjectively categorized as low, moderate or high by the lead pathologist and one other assessor based on the description of the texture and seepage during initial cutting. Fibrosity of the blubber was similarly assessed based on texture by the lead pathologist and one other assessor at necropsy (Raverty *et al*., 2024). Fibrous blubber is dense and the network of fibres is distinguishable from non-fibrous blubber which presents a spongier and softer texture when palpated. Additionally, SON was chosen as a comparative metric. This open-source guideline for ranking of nutritional condition ranges from one to four, with categories of one (emaciated or poor), two (thin or fair), three (average or moderate) and four (fat, good or excellent) (Raverty *et al*., 2024). For this ranking, an experienced pathologist reviewed every available detail on the case including intact carcass appearance; depth and characteristics of the blubber; location, quantity and quality of subcutaneous fat (e.g. nuchal fat pad); and internal or cavitary fat (associated with membranes and the serosal surfaces of organs in the thoracic and abdominal cavities).

## Blubber histology

When possible at first field response to a reported whale carcass either floating in the bay or beach-cast, a sample of the integument (epidermis to the superficial fascia) ~10 $cm^2$ on the surface was dissected from the mid-lateral flank immediately caudal to the axilla. In the laboratory, a subsample of this, ~2 × 1 cm at the surface and full depth (usually less than 12 cm) was removed and fixed in 10% neutral buffered formalin for a minimum of 48 h. After fixation, three sections were selected and placed in standard histology cassettes representing the layers (i) epidermis, dermis and superficial hypodermis (blubber), (ii) a vertical plane section of mid hypodermis and (iii) a vertical section of the deepest level of the hypodermis (Fig. 3). The cassettes were processed to paraffin, sectioned at 5 μm and stained with H&E following standard histology protocols. On microscopy,

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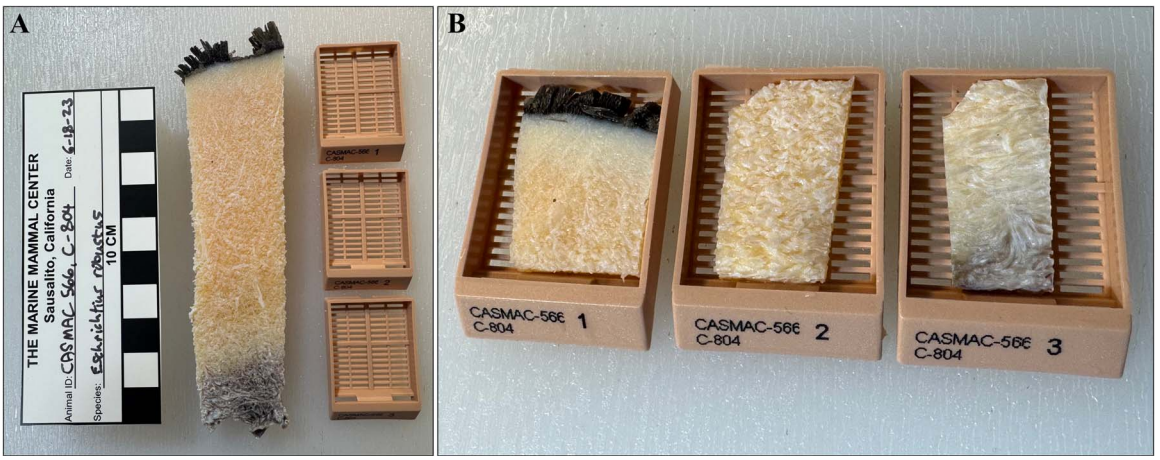



**Figure 3:** Blubber sample trimming example for histology preparation. Panel A shows the intact formalin-fixed blubber sample, while panel B shows vertical sub-samples of the three layers (superficial shown in cassette one, middle shown in cassette two and deep shown in cassette three). Dorsal to ventral orientation for each is determined by the location of the epidermis in cassette one and a diagonal notch for cassettes two and three indicating the top of the sample.

a representative area of each slide was selected and photographed at 40× and 100× magnification. The 100× image was used to verify the morphology and cell types in each section while the 40× image was used to visually estimate the percentage of area occupied by vacuolated (presumed lipid-filled) adipocytes in each layer, and each assigned a 10-percentage-point bin (i.e. 0–10%, 10–20%, 20–30%, 30–40% … 90–100%). The bins were assigned by lead pathologist P.J.D. and discussed in-person with author J.M.S. until agreement was reached in all cases, although there were no notable disagreements.

## Analysis

We conducted Spearman rank correlations between the mean of the two raters' °BC measurements and each rater's Bradford scores to assess correspondence between the two BC methods. Subsequent analyses used the scores from the rater with the highest agreement to the °BC mean. Exploratory analysis using scores from the other rater produced no differences in the significance of model outcomes.

We used regression-based models to examine associations between a whale's live Bradford score or °BC and the following necropsy-derived metrics: whether blubber was described as fibrous (binary, Y/N), blubber oil (ordinal, low/moderate/high), blubber depth (continuous; dorsal, ventral, lateral), SON (ordinal, emaciated/thin/average/good) and adipocyte percentage bins at deep, middle and superficial blubber layers. Missing data were handled using pairwise deletion, so that only observations with complete data for each response-predictor combination were included in a given analysis.

Model type was selected based on the structure of the response variable. Binary outcomes were analysed using binomial logistic regression, ordinal outcomes using ordinal logistic regression and continuous outcomes using linear regression. Blubber oil was analysed as a binary outcome for °BC because the data contained two of the three categories, whereas all three categories were represented in the Bradford analysis and were therefore analysed using ordinal logistic regression. For Bradford models of blubber characteristics (fibre and oil), Bradford score 'good' was excluded because it only contained two data points and lacked response variation, resulting in model separation. Statistical significance for binomial and ordinal logistic regression models was assessed using likelihood ratio tests (LRTs), comparing models containing the predictor to corresponding null models. For linear regression models, statistical significance of predictor coefficients was assessed using the associated *t*-tests. Effect sizes are reported as odds ratios (ORs) with 95% confidence intervals (CIs) for binomial and ordinal logistic regression models and as regression coefficients ($\beta$) ± standard error (SE) for linear models. Because sample sizes were small for several response/predictor combinations, effect estimates and CIs were considered alongside significance tests, and nonsignificant results were interpreted as inconclusive rather than as evidence of no association.

To provide descriptive measures of fitted-model performance, F1 scores were calculated for binomial logistic regression models, and macro-averaged F1 scores were calculated for ordinal logistic regression models. Macro-F1 was calculated as the unweighted mean of class-specific F1 scores, thereby giving each response category equal weight. F1 summarizes classification performance based on precision and recall, with values approaching 1 indicating greater agreement between observed and model-predicted classifications. For linear regression models, fitted-model performance was summarized using the coefficient of determination ($R^2$). Given the small sample sizes, these performance metrics were interpreted descriptively and were not considered independent validation of predictive performance. All models were fit using RStudio version 2026.01.2+418, and model assumptions were assessed by visual inspection (RStudio Team, 2025).



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# Results

## Live whale body condition

Out of 21 matched carcasses, 12 had suitable images to measure °BC, and an additional three had suitable images to score under the Bradford methodology. Three images that were suitable for scoring with the Bradford method but not for measuring °BC were those in which the angle of the whale relative to the photographer was too acute, and while the shape of the body was visible the detail required for °BC was not attained. These three images were not used in the comparison between the two live whale metrics, but were included in analysis for necropsy metrics. The number of days that the images were taken prior to the individuals' death ranged from four to 27, with an average of 12 ± 2 days.

We found agreement between our two raters measuring the °BC, with only one photograph problematic due to glare and a slight misfocus. Inter-rater reliability for °BC measurements was moderate to good (ICC[2,1] = 0.66, 95% CI 0.20–0.89). Reliability improved when averaging across raters (ICC[2,*k*] = 0.79, 95% CI 0.33–0.94), and a paired *t*-test indicated no significant difference between raters ($t(11) = 1.21$, $P = 0.25$). Subsequent analyses therefore used the mean of the two raters' °BC measurements due to this high level of agreement, hereafter simply referred to as °BC.

For Bradford scores, inter-rater reliability was evaluated using Cohen's κ. Because scores were ordinal, weighted κ coefficients were calculated. Quadratic weighted κ indicated substantial agreement (κ = 0.79, 95% CI 0.58–1.00, $n = 18$), exceeding both unweighted (κ = 0.62) and linearly weighted estimates (κ = 0.70). Bradford's BC scores from both observers were moderately negatively correlated with mean °BC (Spearman's ρ = −0.42 to −0.47), indicating that higher categorical scores corresponded to lower angle measurements, as expected. Mean BC angle was more strongly associated with rater A.M.W.'s scores (ρ = −0.57, $P = 0.052$, $n = 12$) than with rater J.M.S.'s scores (ρ = −0.41, $P = 0.183$, $n = 12$). Both scores were consistent with the expected inverse relationship between angle and BC; rater A.M.W.'s BC scores were retained for subsequent analyses. The °BC measurements correlated closely with Bradford categories of two and three, but Bradford category one (poor) was found to be associated with a wider variety of °BC measurements (Fig. 4).

Whales in this study varied widely in BC regardless of methodology used to make the assessment. The range of °BC measurements was 2.19–9.32, with a mean and standard error of 5.25 ± 2.39. The Bradford scores from rater A.M.W. were concentrated in the lowest category (median = 1; mode = 1), while rater J.M.S. showed only a slightly higher central tendency (median = 1.5) but shared the same most frequent score (mode = 1), with most observations in categories one and two.

## Necropsy data

The necropsy reports for the 15 whales with suitable BC images were reviewed, and seven of those 15 had full necropsies, four had partial necropsies, and three had only samples collected. One whale was completely inaccessible and therefore was excluded from this study. The whales were either sub-adult ($n = 7$) or adult ($n = 8$) and included 10 males, 3 females and 1 whale of unknown sex. Decomposition ranged from freshly dead to moderately decomposed. Seven whales included in this study were determined to have injuries consistent with blunt and/or sharp force trauma from presumed vessel strike as the cause of death, and the remaining cases did not have a determined cause of death.

In all but one case, the external appearance of the carcass could not be adequately evaluated for BC given that its recumbency was dorsal (belly-up) or lateral. Dorsal and lateral recumbency obscure anatomic features necessary for evaluation of external BC, including the scapulae and dorsal cervical area. The external appearance was therefore recorded but did not factor strongly for the SON determination.

## Blubber depth and characteristics

Blubber depths were found to be variable, with no statistically significant associations detected between either °BC or the Bradford score at any location (Table 1). Linear regression models provided insufficient evidence of an association between °BC and dorsal blubber depth (β = 0.007, $P = 0.982$, $n = 8$) or ventral blubber depth (β = 0.088, $P = 0.888$, $n = 7$). Lateral blubber depth showed a positive, non-significant relationship with °BC (β = 0.327, $P = 0.137$, $n = 10$), opposite the expected direction since higher °BC reflects poorer condition. Similarly, there was insufficient evidence of associations between Bradford rating and blubber depth at any sampling location. Compared with Bradford-rated poor whales, fair whales had lower estimated dorsal (β = −3.24, $P = 0.239$, $n = 11$), lateral (β = −1.31, $P = 0.477$, $n = 14$) and ventral blubber depth (β = −0.13, $P = 0.973$, $n = 11$). Although all relationships were negative in direction, suggesting that whales rated in better condition had lower estimated blubber depths, the uncertainty associated with these estimates precluded definitive conclusions regarding an association.

Similarly, there was insufficient evidence of associations between qualitative blubber characteristics and °BC (Table 2). Higher °BC was associated with lower estimated odds of fibrous blubber (OR = 0.64, $P = 0.209$, $n = 10$), and moderate blubber oil classification (OR = 0.73, $P = 0.347$, $n = 10$), although uncertainty in these estimates is notable. Bradford 'good' whales contained only two observations and lacked variation/overlap across the response categories, preventing reliable estimation of its effect; these were therefore excluded from the qualitative blubber characteristic models. Among whales rated 'poor' or 'fair', there was insufficient evidence of an association between Bradford score and fibrous blubber or blubber oil. Compared with poor whales, fair whales had lower estimated odds of fibrous blubber (OR = 0.33, $P = 0.415$, $n = 13$), and higher estimated odds of being in a higher blubber oil category (OR = 1.70, $P = 0.728$, $n = 13$), though the effect estimates are imprecise.

## State of nutrition

SON was significantly associated with live BC measurement, °BC. Whales with lower °BC had significantly higher SON (LRT $\chi^2_1 = 9.54$, OR = 0.28, $P = 0.002$, $n = 9$; macro-F1 = 0.50). Higher °BC values were associated with lower SON categories, corresponding

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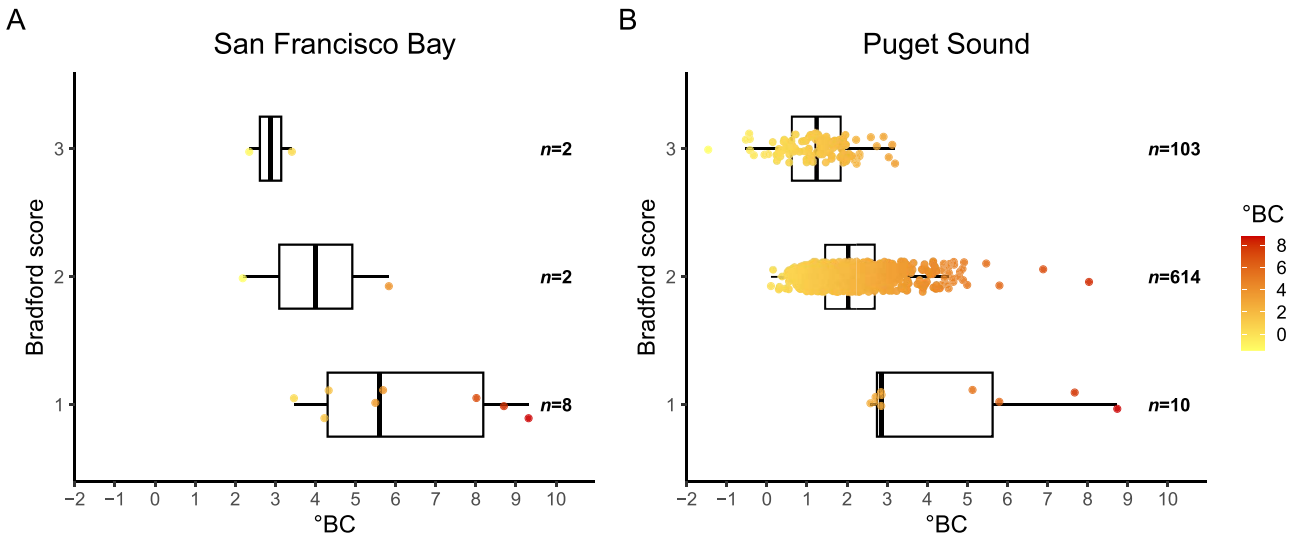



**Figure 4:** Photographs that were given both °BC measurement and a Bradford score by A.M.W. from whales in this study (A) and from previously published data in Puget Sound (B, Telford *et al*., 2026). Data in panel B includes repeated measurements of the same individuals throughout a feeding season, while panel A represents only one measurement from each individual. Boxplots for each category indicate the median, interquartile range and outliers. Each point of data is represented and shaded along a gradient, where yellow is the lowest °BC and red is the highest °BC, corresponding to a worsening condition.

**Table 1:** Results of linear regression models examining relationship between live whale BC measurements and necropsy-derived blubber depth (BD)

| Predictor | Outcome | *n* | β ± SE | *P*-value | $R^2$ |
|---|---|---|---|---|---|
| Bradford | Lateral BD | 14 | −1.57 ± 0.960 | 0.127 | 0.183 |
| °BC | Lateral BD | 10 | 0.327 ± 0.198 | 0.137 | 0.254 |
| Bradford | Dorsal BD | 11 | −1.43 ± 1.84 | 0.457 | 0.063 |
| °BC | Ventral BD | 7 | 0.088 ± 0.593 | 0.888 | 0.004 |
| Bradford | Ventral BD | 11 | −0.111 ± 2.29 | 0.962 | <0.001 |
| °BC | Dorsal BD | 8 | 0.007 ± 0.285 | 0.982 | <0.001 |

Predictors include live whale metrics °BC and Bradford score (Bradford); outcomes include lateral, ventral and dorsal blubber depth. Effect estimates are reported as regression coefficients (β) ± standard error (SE), and $R^2$ is reported as a descriptive measure of fitted-model performance.

to poor nutritional condition and consistent with expectations (Fig. 5).

In contrast, Bradford scores did not predict SON (OR = 1.78, $P$ = 0.607, $n$ = 13; Table 2). There was one whale for which the Bradford score was the lowest, and their SON was the highest ranking (Fig. 6). Together these results suggest that while both live BC metrics are associated in the expected biological direction with respect to SON, °BC may provide a more statistically robust predictor than the categorical Bradford score.

## Blubber histology

Each of 14 whales with blubber histology available from sampling had markedly lipid-depleted adipocytes at the deep layer, ranging only from 0 to 10% filled. Deep adipocyte fill was therefore not analysed in statistical models because the data exhibited insufficient variation. Adipocytes from the mid-level blubber depth ranged from 10 to 60% filled, while those in the most superficial level had the most variation, from 10 to 90% filled (Fig. 7). Adipocyte fill in the middle blubber was significantly associated with °BC (LRT: $\chi^2_1$ = 5.31, OR = 0.21, $P$ = 0.021; macro-F1 = 0.52; Table 2). Higher °BC values were associated with lower adipocyte fill categories, indicating reduced lipid storage within the middle blubber layer. In contrast, °BC did not significantly predict adipocyte fill in the superficial blubber layer (OR = 0.76, $P$ = 0.348). Bradford score did not significantly predict adipocyte fill in either the middle (OR = 0.46, $P$ = 0.426) or superficial blubber layers (OR = 0.43, $P$ = 0.247; Table 2).

# Discussion

Here, we found that the new lateral image BC methodology °BC was associated with the necropsy index SON, supporting its potential as



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**Table 2:** Results of logistic and ordinal logistic regression models examining relationships between live whale body condition measurements and categorical necropsy-derived variables

| Predictor | Outcome | Model | *n* | OR (95% CI) | *P*-value | F1 |
|---|---|---|---|---|---|---|
| °BC | SON | Ord. logistic | 9 | 0.28 (0.05–0.68) | 0.002* | *0.5* |
| °BC | Mid Adipo | Ord. logistic | 11 | 0.21 (0.03–1.54) | 0.021* | *0.519* |
| °BC | Fibre | Logistic | 10 | 0.64 (0.25–1.27) | 0.209 | 0.800 |
| Bradford | S Adipo | Ord. logistic | 14 | 0.43 (0.1–1.83) | 0.247 | *0.085* |
| °BC | Oil | Logistic | 10 | 0.73 (0.32–1.42) | 0.347 | 0.875 |
| °BC | S Adipo | Ord. logistic | 11 | 0.76 (0.41–1.40) | 0.348 | *0.199* |
| Bradford | Fibre | Logistic | 13 | 0.33 (0.01–4.68) | 0.415 | 0.706 |
| Bradford | Mid Adipo | Ord. logistic | 14 | 0.46 (0.06–3.73) | 0.426 | *0.182* |
| Bradford | SON | Ord. logistic | 13 | 1.78 (0.19–17.52) | 0.606 | *0.276* |
| Bradford | Oil | Ord. logistic | 13 | 1.70 (0.09–55.09) | 0.728+ | *0.290* |

Predictors are live whale metrics °BC and Bradford score (Bradford); outcomes include SON, blubber fibre, blubber oil, and adipocyte fill at the middle (Mid Adipo), and superficial (S Adipo) blubber layers. Effect sizes are reported as OR with 95% CIs. F1 scores are included as descriptive measures of fitted classification performance, with higher values indicating greater agreement between observed and model-predicted classifications. Italics indicate macro-F1 for ordinal outcomes, calculated as the unweighted mean of class-specific F1 scores. Significant findings are shown in italics. Reported *P*-values are unadjusted, significant results indicated with *.

+The Bradford–blubber oil model showed sparse-data/separation behaviour that prevented reliable estimation of the odds ratio and profile-likelihood confidence interval; the overall *P*-value is from the likelihood ratio test.

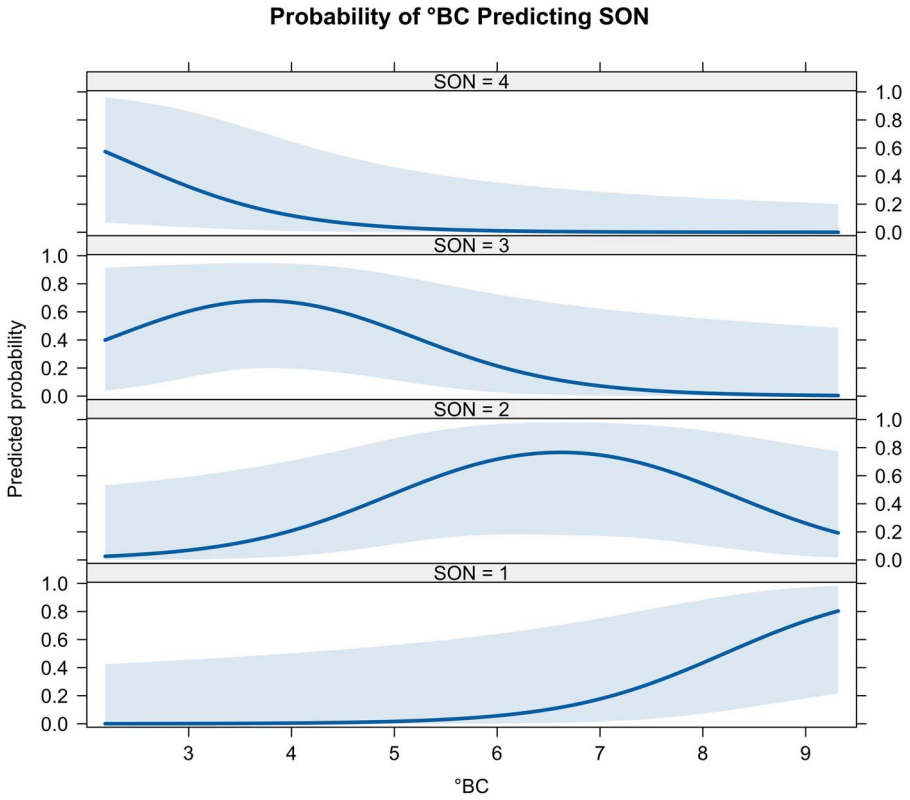



**Figure 5:** The predictive ability of °BC for each category of SON displayed here with light blue bands of 95% CIs.

a biologically meaningful indicator of nutritional status. Additionally, we found that manually estimated adipocyte fill at the middle blubber layer was predicted by °BC, providing additional evidence that °BC reflects aspects of the nutritional condition of carcasses even without a complete internal necropsy. This study represents, to our knowledge, the first comparison of live large whale BC assess-

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**Figure 6:** Whales with live body condition Bradford scores of one and two (A and D, respectively) along with photographs of their subcutaneous and mesenteric fat present during necropsy. All photographs of the individual with Bradford score '1' are boxed in red, and all photographs of the individual with Bradford score '2' are boxed in blue. In panel A, the prominence of the post-cranial depression is indicated by the black arrow and the presence of a post-cranial hump is indicated by the white arrow. In panel D, the post-cranial depression is indicated by the black arrow. Panel B shows ample subcutaneous fat between the blubber layer and body wall, indicated by arrows, and C shows visible deposits of mesenteric fat of the individual in panel A, indicated by arrows and resulting in a good SON. Panel E shows moderate subcutaneous fat of the individual in panel D, resulting in a thin SON. Panel F shows the individual's mesentery at an advanced stage of decomposition, preventing the evaluation of mesenteric fat.

ment methodologies against necropsy metrics in the same individuals. We address a previously identified research gap in large whale physiology to ground-truth methodology of BC assessment methods (Curran & Asher, 1974; Evans *et al*., 2003; Stevenson & Woods, 2006; Hart *et al*., 2013; Williams *et al*., 2013; Wilder *et al*., 2016; Kershaw *et al*., 2017, 2019; Castrillon & Nash, 2020; Christiansen *et al*., 2020; Raverty *et al*., 2020; Larrat & Lair, 2022; Cicciarella *et al*., 2026). Future studies across the grey whale's range could further evaluate °BC methodology to gain more fine-scale data of individual BCs from lateral images.

Data from the same individuals while living and dead are rare, and the associations identified here provide useful preliminary evidence despite the modest sample size. However, it is important to interpret results cautiously given the sample size and the potential for sparse distribution among ordinal categories, in some cases. The individuals included in this study constitute a variety of causes of death, reducing the likelihood that the dataset reflects a single mortality process (Christiansen *et al*., 2020; Lowe *et al*., 2021). It is possible, however, that whales in poorer BC are more susceptible to anthropogenic mortality. Grey whales in SF Bay face intense anthropogenic hazards, and their occurrence in this bay has been hypothesized to be driven primarily by malnutrition (Gulland *et al*., 2005; Slaathaug *et al*., 2026). The BC of whales in this study ranged from poor to good as scored by the Bradford method, though notably most were in poor condition with depleted fat reserves resulting in a visible post-cranial depression. No whales measured °BC < 2, in contrast to whales measured on the foraging grounds of Puget Sound across the season (Telford *et al*., 2026). However, a few were found to be in what we suspect to be a reasonable BC following a prolonged period of fasting associated with the northbound migration, given historical literature from whaling which referenced body fat depletion of whales in this region at this stage of migration (Rice *et al*., 1971). An increased sample size would strengthen inference of overall nutritive state among whales utilizing this habitat and may allow further elucidation of prey availability. Future studies could employ the use of °BC and/or UAS photogrammetry to examine intra-annual change of individual BC to further understand potential nutritional gain from this habitat, replicating the examination of grey whales utilizing Puget Sound to forage (Telford *et al*., 2026). It is possible that grey whales utilizing SF Bay are not able to consume prey items that improve their BC significantly, or that they are potentially killed prematurely while in the process.

We found that the two live whale BC methodologies evaluated, Bradford score and °BC, were associated with each other as expected. When examining the data distribution of °BC within each Bradford score category, we observed greater overlap in °BC values among poorer Bradford score categories, suggesting reduced discrimination among lower-condition animals. This result was mirrored in findings from grey whales evaluated using both methodologies in Puget Sound (Telford *et al*., 2026; Fig. 3). Due to this, we consider that the Bradford method may not account for differences in the shape of the post-cranial area among individuals, which may become exacerbated as fat is depleted (Lockyer & Waters, 1986; Koopman *et al*., 2002;

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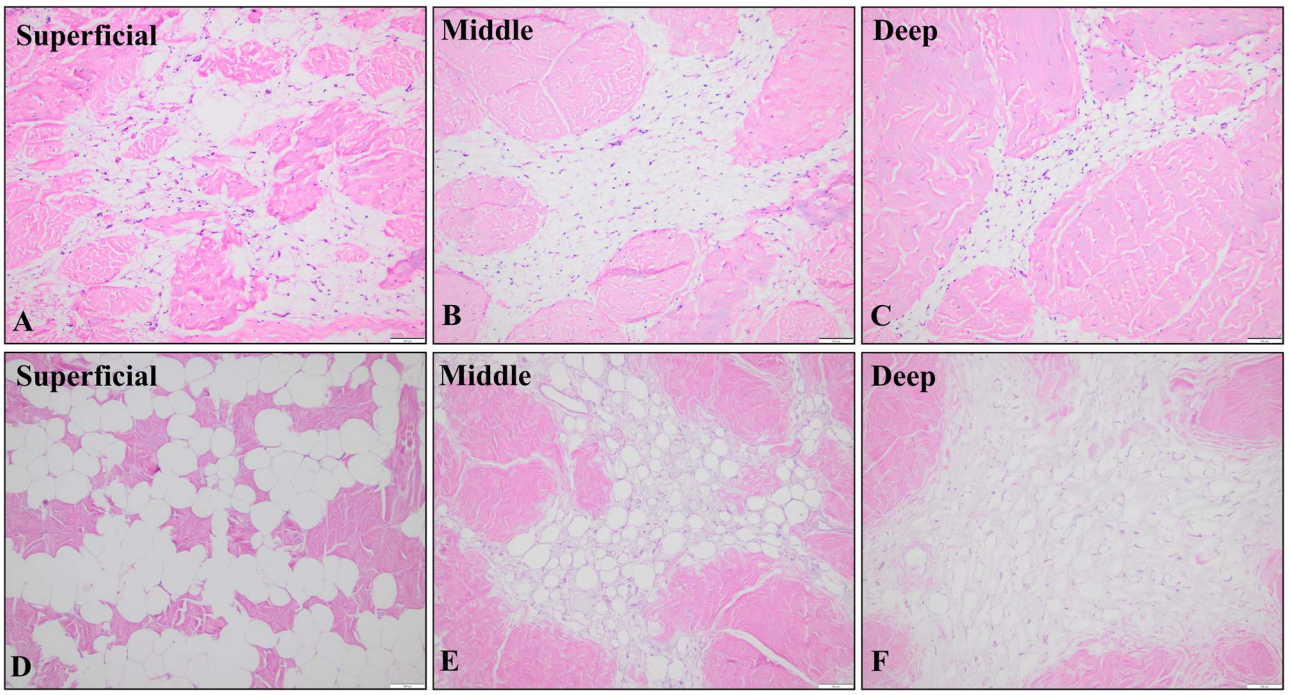



**Figure 7:** Histology images at 100× magnification from the three blubber strata of a whale with depleted adipocytes (A–C) and a whale with filled and robust adipocytes in the superficial and middle layers (D & E) and more depleted adipocytes in the deep layer (F). The appearance of contracted or collapsed adipocytes is marked by more visible and closely apposed cell membranes and nuclei (blue/purple), while lipid-filled adipocytes appear white.

Telford *et al*., 2026). Additionally, fat loss may not occur uniformly across individuals and therefore be reflected in the early appearance of a PCH anterior to the cervical depression which would result in a whale being rated poor under Bradford methodology but retaining a low °BC. Contrastingly, the °BC allows for a sensitive measurement of severity of the cervical depression that captures finer-scale variation compared to gross morphology (Telford *et al*., 2026). We found insufficient evidence of associations between Bradford score and the necropsy or histology metrics examined, in contrast to the associations identified with °BC. Together, these findings suggest that quantitative assessment of cervical depression may capture finer-scale variation than categorical Bradford scores, although this pattern should be evaluated in larger datasets. It is important to consider, however, that the nature of data collection for this study was primarily opportunistic or for the purpose of photo-identification for another study (Slaathaug *et al*., 2026). Future studies could improve upon our methodology by incorporating angle measurements from multiple photographs of the same individual on the same observation day and include error in modelling approaches.

The SON index score and °BC were found to be significantly associated. The SON index for grey whales is openly available, with photographs to guide on ranking each category (Raverty *et al*., 2024). Necropsy data is by nature descriptive and usually subjective, capturing more nuances and observations than one measurement alone, thus often creating a challenge for broad-scale analysis (Lennon *et al*., 2025). We hypothesize that the SON index is made stronger by its use of characteristic and descriptive data as well as direct measurements, and its ability to synthesize all metrics into one determinative score (Raverty *et al*., 2020, 2024; Lennon *et al*., 2025). The SON index does include a category for evaluating the external appearance of a carcass, though we do not consider that to be heavily influential in the association found in this study due to carcass recumbency precluding the evaluation of external body shape in almost every case. Bloating and gravity can also significantly alter the appearance of external morphology post-mortem. The ability of necropsies to characterize internal fat presence may be particularly informative for the evaluation of nutritional status, as the fat present on organs and subcutaneous fat between the blubber layer and body wall may be more metabolically active compared to fat stored within the blubber layer itself. Our findings align with pathological consensus suggesting that internal fat stores and total fat, as determined through rendering in whaling-era research, may reflect energy available and indicate BC more reliably (Víkingsson, 1995; Niæss *et al*., 1998; Raverty *et al*., 2020). Furthermore, since the nuchal crest area is an accumulation point of internal fat stores, it follows that a whale rated in better condition due to the angle of cervical depression may have more description of internal fat present, resulting in a higher SON. The nuchal fat pad is visible in grey whales during necropsy and changes texture, volume, colour and general appearance with the amount of fat stored (Figs S1 and S2). Decomposition is a notable challenge for adequate examination of internal fat and for carcasses higher than a decomposition score of three, this assessment is likely impossible.

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We found no evidence of association between blubber depths or characteristics and either of the live whale metrics. Blubber depth was found to be highly variable by location in the same animal, aligning with previous studies demonstrating that blubber thickness is not homogenous across the body and is influenced by other factors such as reproductive status, age and total length (Lockyer & Waters, 1986; Miller *et al*., 2011). It has also been shown that blubber depth, when examined alone, does not provide a reliable indication of BC and that depth loss varies by site in emaciated cetaceans (Koopman *et al*., 2002; Evans *et al*., 2003; Raverty *et al*., 2020). Heterogenous fat loss is further evidenced by our findings of contrasting blubber depth trends. Blubber has critical functions in addition to lipid storage, such as thermoregulation and maintaining hydrodynamic shape, and in cetaceans the primary function differs by layer/strata (Aguilar & Borrell, 1990; Koopman *et al*., 2002; Struntz *et al*., 2004; Strandberg *et al*., 2008). Blubber depth measurements can also have error based on sampling methodology such as expansion when cut (Castrillon & Nash, 2020). Additionally, blubber characteristics recorded at necropsy are subjective, determined by the pathologist or prosector and unstandardized. Our decision to evaluate these metrics while understanding their subjectivity was for the aim of examining all potential indications of a whale's BC available at necropsy. Our results provided insufficient evidence that described blubber characteristics of oil or fibrous texture are representative of live whale BC on their own, though the synthesis of these characteristics together is considered when determining SON.

We found a significant association between °BC and visually estimated adipocyte fill in the middle blubber layer, while evidence of an association in the superficial layer was inconclusive. This is consistent with findings from adult grey whales in Laguna San Ignacio, where adipocyte area in superficial blubber did not differ among photographically assessed BC categories (Magallon Flores *et al*., 2024). Our estimation of the adipocyte fill in each blubber layer was a very simple visual assessment by an experienced pathologist and only requires the collection of one full-thickness blubber sample to perform. This finding has important implications for the field, including that very limited sampling, in this case only one full-thickness blubber sample may provide useful information about an individual's BC from basic histology imaging. However, the wide CI surrounding the middle-layer effect estimate indicates substantial uncertainty, and this association should therefore be interpreted cautiously given the small and unevenly distributed sample. Our results are consistent with previous work indicating that adipocyte metrics may be more dynamic within the middle and deep blubber layers than the superficial layer (Belanger *et al*., 2025; Gómez-Campos *et al*., 2011; Phipps *et al*., 2023; Magallon Flores *et al*., 2024). The grey whale's life history and seasonal feeding strategy requires building lipid reserves to utilize while fasting during a long migration and stay at the breeding grounds (Rice *et al*., 1971; Aguilar & Borrell, 1990; Swartz, 2018). The superficial blubber layer differs in structure from the middle and deep layers, containing a greater proportion of connective and structural tissue and serving a comparatively greater structural role (Struntz *et al*., 2004; Phipps *et al*., 2023). Depleting lipid content of adipocytes in the superficial layer of blubber may be a physiological last resort, as it could alter the body shape beyond what is optimal to maintain a hydrodynamic and therefore energy-efficient state (Struntz *et al*., 2004; Strandberg *et al*., 2008). We were unable to statistically evaluate the relationship between °BC and adipocyte fill in the deep layer due to the finding that the deep layer of each of the whales in this study was severely depleted (0–10% filled). However, this is unsurprising for whales on their northbound migration as the deep layer can be depleted during fasting. The depletion may have been further exacerbated by the coinciding Unusual Mortality Event for this population of Eastern North Pacific grey whales (declining by >50% from 2016 to 2025), with findings of malnutrition across the range (Raverty *et al*., 2024; Eguchi *et al*., 2025).

Obtaining quality necropsy data presents many challenges. Often, carcasses wash ashore in locations that prohibit necropsies due to land management restrictions or preferences. In SF Bay and other urban areas, floating carcasses need to be towed to an area suitable for a full necropsy which in turn is a process limited by resource availability, weather and space availability (Slaathaug *et al*., 2026). Carcasses included in this study were examined to varying extents, from blubber sampling only to full necropsies. Decomposition affects the quality of data available for collection during a necropsy, as evidenced by the rapid decomposition of mesenteric fat (Fig. 6). It is possible that this decomposition altered the accuracy of necropsy or histology assessments in this study, since whales in moderate decomposition state were included. Given the limited sample size, we were unable to robustly evaluate decomposition state or the interval between live photographic assessment and necropsy as potential covariates. Future studies or further analysis should consider limiting individuals based on decomposition state, or incorporate these factors into modelling approaches when sample sizes allow. While our findings provide preliminary evidence linking BC of grey whales using live assessment (°BC) and necropsy-derived metrics (SON and blubber histology), fat storage and usage likely varies by species and further evaluation across cetaceans would be invaluable (Koopman *et al*., 2002; Miller & Hall, 2012; Castrillon & Nash, 2020). Additionally, revisiting and examining these variables in the future with an expanded dataset may illuminate relationships among variables that are not clearly evident in our small sample size.

While lateral image BC analysis is not as sensitive as UAS photogrammetry, it is sensitive enough to detect changes in condition on time scales as short as 11–12 days for some species (Pettis *et al*., 2017). Lateral image analysis is also valuable because it can be applied retroactively to historic long-term databases which do not have UAS imagery, and it remains congruent with UAS-based methods as both generally lead to the same conclusions about an individual's nutritional status (Telford *et al*., 2026). While many future studies will focus on utilizing UAS imagery to conduct BC analyses, we should still consider lateral images a beneficial tool for historic datasets and areas with limited resources to conduct the highly skilled and resource-intensive operations necessary for reliable photogrammetry analysis. Additionally, in areas where UAS activity is not permitted, lateral images provide biologically meaningful data for BC examination.

In conclusion, we found that °BC was associated with both a necropsy-derived nutritional index and middle blubber layer adipocyte histology. Internal fat examination proved especially biologically meaningful and may offer the closest possible assessment

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of readily available, metabolically active energy stores in grey whales. Given the implication of individual BC examination on long-term studies of population and ecosystem health, developing validated and reliable methodologies is critical (Castrillon & Nash, 2020). Because lateral photography is inexpensive, non-invasive and available from long-term photo-identification catalogues, these methods offer a rich source of data for evaluating individual nutritional status and health across large temporal and geographic scales. This study adds preliminary evidence to support the use of °BC as a sensitive, inexpensive and non-invasive method to retrospectively evaluate BC in historical datasets and to compare health of live whales across populations. Though the sample sizes in this study are small, datasets of this nature are extremely rare and this investigation is novel. Interpretations of these results should therefore be treated cautiously and provide a starting ground for the direction of additional studies utilizing °BC. Investigating the relationship between °BC estimates from live whales and key necropsy results also highlights the importance of SON and adipocyte fill in the middle layer as particularly informative metrics for assessing nutritional status in dead grey whales. These findings identify promising connections between pre- and post-mortem BC assessment methods and support further evaluation of their comparability. This advancement contributes to ongoing efforts to improve the ability of energy reserve assessments to infer consequential information regarding individual health and reproductive viability (Sæther, 1997; Miller *et al*., 2011; Williams *et al*., 2013; Christiansen *et al*., 2014; van Aswegen *et al*., 2024). Future studies could test whether these associations are reproducible in other populations and species, expand the use of °BC to other studies to further determine reproducibility or aim to implement a similar methodology improvement as °BC for their target study species.

## Acknowledgements

Thanks go to the efforts of all necropsy staff, fellows, interns and volunteers from the California Academy of Sciences and TMMC. A special thank you to members of the cetacean conservation biology department at TMMC, specifically Norely Faz and Gina Lonati for compiling the photographs of the whales used in this study, along with Bill Keener, Marc Webber and Kathi George for their support of this project. Additional thanks go to Kate High for conceptual support and providing relevant necropsy images.

## Author contributions

J.M.S.: Conceptualization, Data Curation, Formal Analysis, Funding Acquisition, Investigation, Methodology, Project Administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, review and editing. P.J.D.: Conceptualization, Investigation, Methodology, Project Administration, Resources, Supervision, Visualization, Writing-original draft, review and editing. K.A.T.: Investigation, Methodology, Resources, Visualization, Writing-review and editing. M.F.: Funding Acquisition, Investigation, Resources, Writing-original draft, review and editing. A.M.W.: Investigation, Writing-original draft, review and editing. A.G.: Visualization, Writing-original draft, review and editing. R.S.L.: Supervision, Visualization, Writing-original draft, review and editing. B.H.: Conceptualization, Investigation, Writing-review and editing. J.C.: Conceptualization, Project Administration, Resources, Supervision, Writing-review and editing. D.E.C.: Conceptualization, Data Curation, Formal Analysis, Funding Acquisition, Investigation, Methodology, Project Administration, Resources, Software, Supervision, Validation, Writing-original draft, review and editing.

## Conflicts of interest

The authors have no conflicts of interest to disclose.

## Funding

This work was supported by The National Science Foundation's Graduate Research Fellowship Program (DGE-2437852 to J.M.S.) and two John H. Prescott Marine Mammal Rescue Assistance Grants awarded to the California Academy of Sciences (NA19NMF4390150 and NA23NMF4390335).

## Data availability

The data that support the findings of this article are openly available in Figshare at doi: 10.6084/m9.figshare.32249673.

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