Marine Mammal Science

ARTICLE OPEN ACCESS

How Robust is *Eschrichtius robustus*? A Novel Photographic Index of Body Condition From Boat-Based Photographs of Gray Whales

Kira A. Telford[1] | John Calambokidis[2] | Kiirsten R. Flynn[2] | Jasmine Witt[1] | Alie Perez[2] | John W. Durban[3] | Holly Fearnbach[3] | Erin L. Meyer-Gutbrod[1]

[1]University of South Carolina, Columbia, South Carolina, USA | [2]Cascadia Research Collective, Olympia, Washington, USA | [3]SR3, SeaLife Response, Rehabilitation and Research, Des Moines, Washington, USA

Correspondence: Kira A. Telford (ktelford@seoe.sc.edu)

Received: 27 January 2025 | **Revised:** 5 September 2025 | **Accepted:** 22 September 2025

Funding: This study was supported by University of South Carolina Magellan Scholar and Honors College grants awarded to J. Witt. Drone photogrammetry was authorized by NMFS Research Permit 19091, and supported by SR3 and the NOAA Fisheries UME Working Group.

Keywords: body condition | eastern North Pacific gray whales | mixed effects models | photogrammetry | photo-identification | Puget Sound

ABSTRACT

Although the eastern North Pacific gray whale (*Eschrichtius robustus*) population has recovered from population declines associated with whaling, they are closely monitored, especially in association with Unusual Mortality Events. Metrics to improve assessment of the health of individual animals, when averaged, are valuable to inform monitoring and management. We used 30 years of photographic data of a unique gray whale feeding aggregation to develop and test a new methodology for assessing body condition. This group of individuals (20 as of 2021, but 11 in the study group), known as the Sounders, regularly enter Puget Sound, Washington, USA, to forage on ghost shrimp in the spring and early summer. Almost 35,000 images were examined and 729 were selected as being suitable to assess individual body condition. Geometric measuring tools in open-source image analysis software were used to measure a novel body condition angle, °*BC*, as a proxy for changes in blubber thickness. This °*BC* varied significantly with the day of the year, with increases in blubber thickness observed as individuals progressed through the feeding season. Other metrics, such as year and surfacing interval, were not found to have a significant effect on °*BC* within this dataset. This novel index of body condition illustrates the opportunity to develop new methods to quantitatively assess change in individuals at both seasonal and annual scales. Expansion of this method to the larger eastern North Pacific gray whale population may allow for a more detailed examination of fluctuations in body condition to better understand both environmental and anthropogenic impacts. There is also potential for adaptation of the method to apply to historic photo catalogs of other baleen whale species, creating opportunities for enhanced data-driven management plans.

1 | Introduction

Objective and quantitative indicators of body condition and health are critical components of ecosystem-based management and conservation of protected species (Pettis et al. 2017; Riisager-Simonsen et al. 2020; Stewart et al. 2021). To assess cumulative environmental conditions and threats throughout a species' range, a body condition index can be used to track the foraging success of a particular population by monitoring changes in body condition across seasons (Christiansen et al. 2020; Fearnbach et al. 2020; Torres et al. 2022). Health assessments can be used to evaluate the impact of natural environmental drivers, as well as anthropogenic factors such as vessel traffic and entanglements, on the body condition of individuals in a cetacean population, both seasonally and annually, to better increase our understanding of ecosystem-wide processes (Akmajian et al. 2021; Blair et al. 2016; Castellote et al. 2012; Ingman et al. 2021; Johnson et al. 2005; McHuron et al. 2021; Pettis et al. 2017; Saez et al. 2021; Silber et al. 2021; Stewart et al. 2021; Wachtendock et al. 2022).

Most baleen whale species are capital breeders, relying on an accumulation of fat stores during summer foraging in high latitude feeding grounds to supplement them throughout their migration to mating and calving grounds in lower latitudes (Bengtson Nash et al. 2013; Eisenmann et al. 2016; Young 1976). Without a successful foraging season, individuals may experience a decline in body condition, potentially resulting in increased disease transmission and/or reproductive loss (Pettis et al. 2017; Stimmelmayr and Gulland 2020). Poor body condition occurs when individuals are not able to build necessary blubber reserves, and their body condition status can serve as a proxy for identifying ecological fitness and as an indicator of the health of the ecosystem (Riisager-Simonsen et al. 2020).

The gray whale (*Eschrichtius robustus*) is a filter feeder that spends its foraging season in high latitudes where ecosystem productivity is greater and then migrates to lower latitudes during the winter months to breed and calve (Pike 1962). Two distinct populations of North Pacific gray whales are currently recognized (NOAA Marine Mammal Stock Assessment Report: Western North Pacific Stock 2020b (primarily occurring along the coast of China and Russia and considered endangered with less than 300 individuals (Bröker et al. 2020)) and Eastern North Pacific Stock 2020a). The eastern gray whale stock migrates from their northern feeding grounds in the Bering, Chukchi, and Beaufort seas to their southern wintering grounds in Baja California, Mexico, and numbers ~15,000 individuals following a recent decline in abundance (Christiansen et al. 2021; Durban, Fearnbach, et al. 2015; Durban, Weller, et al. 2015; Stewart and Weller 2021; Stewart et al. 2023). Within this larger eastern population, there is a distinct subgroup of around 230 individuals known as the Pacific Coast Feeding Group (PCFG) that end their northbound migration in the coastal waters off British Columbia and southeast Alaska (Frasier et al. 2011).

The primary prey of the PCFG is amphipods and mysids, and previous studies have documented variation in gray whale health and demography associated with changes in prey abundance (Burnham and Duffus 2022; Darling et al. 1998; Hildebrand et al. 2022; Soledade Lemos et al. 2020). Often prey is affected by ocean processes, such as the Northeast Pacific marine heatwave of 2014–2016, and such changes in environmental conditions can have a cascading effect on the food chain (Roger-Bennett and Catton 2019; Stewart et al. 2023; von Biela et al. 2019; Wachtendock et al. 2022). Poor prey recruitment will negatively impact foraging success, resulting in declines in body condition. Ongoing limitations in prey will ultimately reduce a population's ability to successfully reproduce and/or may lead to starvation and subsequent mortality (e.g., Ward et al. 2009; Meyer-Gutbrod et al. 2015; Stewart et al. 2021).

Declines in prey availability on foraging grounds have resulted in behavioral changes, including shifts in distribution, which may lead to Unusual Mortality Events (UMEs) in gray whales and other baleen whale species (Meyer-Gutbrod et al. 2018; Stewart et al. 2023). Such prey-driven declines may seriously impact vulnerable mysticete populations and increase the threat of extinction (Moore et al. 2022; Meyer-Gutbrod et al. 2021). A UME driven by declines in body condition may also be the result of a species reaching the carrying capacity in their ecosystem and is likely the source of this most recent gray whale UME (Christiansen et al. 2021). In 2016, the Eastern population peaked at nearly 27,000 individuals, but fell to 14,500 individuals in the winter of 2022/23 with a large increase in stranded emaciated whales beginning in 2019 (Eguchi et al. 2023).

Due to difficulties with measuring or tracking changes in feeding rate and success, fluctuations in body condition can be used as a proxy of health since it can be quantitatively measured as an indicator of blubber stores and thus foraging success (Miller et al. 2011). Previously developed methods to assess body condition of gray whales have focused on indicating changes in blubber thickness by describing notable physical features such as the scapula, spine, and the depression behind the post-cranial hump (Bradford et al. 2012; Perryman and Lynn 2002). This body condition index (hereafter referred to as the "Bradford method") has been used as an effective tool to assess gray whale health at the individual and population level (Bradford et al. 2012). The Laguna San Ignacio Ecosystem Science Program has been monitoring the body condition of the gray whales that winter in Laguna San Ignacio for several years using the Bradford method (Valerio-Conchas et al. 2022). They produce annual reports on the status of the population that they photograph. Additionally, the method has been used to study the intra- and interannual body condition changes in the PCFG population (Akmajian et al. 2021; Bierlich et al. 2023).

Although the Bradford method has been used effectively to measure body condition changes in gray whales, there are some limitations. The Bradford method uses a 3-point categorical scale, but since scores are assigned at the researcher's discretion, there is some subjectivity to the scoring. To better understand the full variation in health for gray whales, we propose the development of a more sensitive and objective method that relies on a continuous standardized measurement index, rather than categories as an alternative or a complement to other body condition index methods.

The development of Unmanned Aircraft Systems (UASs), specifically multicopter drones, has created the opportunity for a new technological approach to marine mammal health research (Durban, Fearnbach, et al. 2015; Durban, Weller, et al. 2015; Durban et al. 2016; Christiansen et al. 2016, Koski et al. 2015). Drones provide a vertical aerial perspective of individuals, which allows for photogrammetric analysis of body shape. This has proven to be an effective method of measuring small changes in body condition (Fearnbach et al. 2020) and the efficiency of drones enables measurements of large portions of populations (Christiansen et al. 2021; Stewart et al. 2021).

However, many photographic-identification sighting datasets exist that were collected from boats many years prior to the use of drones (Gendron et al. 2015; Würsig and Jefferson 1990). To accommodate drone limitations in operating capacity and high costs that some researchers face, most photographic data are still collected using standard DSLR cameras rather than drones. To accommodate the large amount of boat-based photographic data, objective photographic measurements are needed when access to a drone is not possible, as well as to provide historic context that includes photographic data collected prior to drone use.

In this study, a photographic technique was developed to measure body condition objectively and quantitatively in gray whales, using a novel metric called the body condition angle (°*BC*). This technique was developed and tested on a small group of whales known as the Sounders that gather annually in Puget Sound between February and June to feed on ghost shrimp (*Callianassa californiensis*). This study focused on 11 individuals that are considered the core group due to their longevity and consistency in visiting Puget Sound. Due to consistent sightings of the Sounders, comprised of 2–10 individuals in a given year over a 31-year monitoring period, this aggregation served as a valuable test group to evaluate individual and temporal effects using this new body condition index. Most of these individuals have been sighted since monitoring began in 1990 by Cascadia Research Collective and return to Puget Sound regularly in the spring seasons (Ballance 2018; Calambokidis et al. 2002; Calambokidis et al. 2010). Occasionally, new individuals are observed, but individuals are not designated as a member of the Sounders aggregation unless they have been observed in the Sound during two consecutive years.

Here we present results from 31 years (1990–2021) of photographic data of the Sounders gray whales using a new method for assessing body condition. Geometric measuring tools in open-source image analysis software were used to assess changes in blubber thickness as a proxy for changes in body condition. We demonstrate the efficacy of this photographic health assessment tool in tracking individual and temporal variation in body condition showing its potential to improve sensitivity in blubber thickness evaluations. As such, this method could be used in future studies to compare the health of individuals in the Sounders aggregation to the health of other gray whales that do not enter Puget Sound or serve as a complement to alternative body condition assessments.

2 | Methods

2.1 | Whale Sighting Data

The photographic identifications and data collected from opportunistic and systemic boat-based surveys of the Sounders gray whales were used in this study. Encounters with Sounders occurred between February and June, with the majority occurring in March and April. Photos collected on these surveys were reviewed and filtered for measurement quality.

As of 2021, the core group of Sounders comprised 8 males and 2 females, and 1 individual of unknown sex, all of which had been sighted in 14–27 years since the start of monitoring in 1990. Individual gray whales are identified by unique pigmentation or scarring patterns on their dorsal flanks and fluke, as well as by their knuckle count and shape (Darling 1984; Weller et al. 1999). The head of an individual can be identified using sequence shots when the individual cannot be identified using traditional marks. The exact age of individuals is unknown, but photogrammetry measurements have shown all individuals to be adult size (Fearnbach et al. 2020, unpublished data). Neither female has been sighted with a calf in Puget Sound, but gap years have been documented when they have given birth and may have continued migrating north to their Arctic feeding grounds with their calf instead of stopping in Puget Sound.

2.2 | Body Condition Angle (°BC)

Bradford et al. (2012) created a three-category assessment focusing on the post-cranial region, the scapula, and the dorsal flanks. While gray whales are typically identified from photographs by pigmentation patterns along their dorsal flanks, variation in blubber thickness in this region is less obvious. Depletion of subcutaneous fat in the post-cranial region results in a post-cranial depression, which is considered to be representative of a cetacean in poor body condition with less-than-optimal blubber reserves (Bradford et al. 2012; Joblon et al. 2014; Pettis et al. 2004). In the present study, we therefore focused measurements on the depth of the depression behind the post-cranial hump, as it shows changes in blubber thickness and is a common part of the whale opportunistically captured in photo-identification images. We developed a new technique that serves as a proxy for quantifying blubber thickness at the post-cranial hump using boat-based photographs to create a more sensitive and objective gray whale body condition index.

Digital and film photos from encounters with Sounders were examined and images of high quality (i.e., resolution, focus, distance to the individual, and lighting) were selected for use where the line of the whale's body was most evident. The best body condition index was measured from high-resolution images in which the estimated distance between the photographer and the whale was minimal, as reduced distance increases photo resolution. Photographs were not collected specifically for this study, and most images taken during an encounter were of lateral flanks or flukes; thus only a small portion of images included the full head anatomy. Photos deemed usable were sorted based on an index of estimated offset angle, which consists of 10° bins representing the estimated angle of the individual from the boat. This index ranged from 0 for individuals parallel to the boat (−5° to 5°) to 9 for individuals perpendicular to the boat (85°–95°). Images with a higher offset angle index (3 and above) were excluded from subsequent analysis, as photos with offset angles of 3 or greater begin to lose precision because °*BC* is most visible and accurate when the animal is nearly parallel with the observation platform.

ImageJ, an open access photo-editing software (Schneider et al. 2012), was used to implement a novel method to measure the post-cranial depression. This method uses the ImageJ "angle tool" to create a new measurement called the body condition angle (°*BC*). An initial measurement (*L*) used to standardize between photos was taken using the "straight-line tool". The *L* line measures from the top of the blowhole to the forward most top point of the post-cranial hump. This measurement is then doubled (*2L*) to find a reference point along the back (*B*) that will be used to measure the °*BC* (Figure 1). The anchor point along the back (*B*) will be standardized to the same position on an individual whale, minimizing changes in angle positioning that may occur from body fluctuations during the breath cycle. Thus, the anchor point (B) on the individual's skeleton is fixed relative to two consistent body reference points: the blowhole and post-cranial hump.

Starting at the anchor point (B), the °*BC* can be taken as the degree of depression behind the post-cranial hump. The mid-point of the angle tool is placed at the top of the post-cranial hump (*PCH*), and the final point, which is the only variable point of the angle measurement, is placed at the lowest point of the depression (*D*) (Figure 2). ImageJ is then used to take a measurement of the °*BC* with precision up to three decimal places. This angle allows the measurement of fine-scale changes in post-cranial depression severity, creating the opportunity for more detailed comparisons between measurements on subsequent photos. A larger °*BC* indicates a deeper depression behind the post-cranial hump and thus corresponds with a thinner blubber layer and worse body condition. A °*BC* on a gray whale with a thick blubber layer would be close to 1 or smaller, sometimes even negative.

Changes in body flexion throughout the dive sequence was considered a variable that could affect measurements, and as such it was assessed by analyzing Sounder dive sequences from photographs collected over a period of 4 days (April 14–17, 2023). Thus, any variation in body condition measurements over such a short period would not be due to significant fluctuations in blubber thickness. To characterize the degree of flexion at different points in a dive sequence, photos were separated into three distinct stages. Stage one includes photos where the whale is rising and the blowhole is higher than the posterior dorsal region in relation to the water's surface; stage two includes photos where the blowhole and posterior region of the whale are approximately equal distances above the water's surface; and stage three includes photos where the whale has begun to resubmerge and the posterior region of the animal is higher than the blowhole. The effects of different offset angles were also analyzed in conjunction with the dive sequence using photos of the most sighted individual within this period.

2.3 | Statistical Analysis

The R environment for statistical computing (R Core Team 2022), implemented within the RStudio software, was used to conduct all analyses. A linear mixed model was used to determine the strength of the relationship between °*BC*, day-of-year, and random effects for year, individual identity, and offset angle of the photograph. Random effects were included in the model as categorical variables. The linear mixed models were fit using

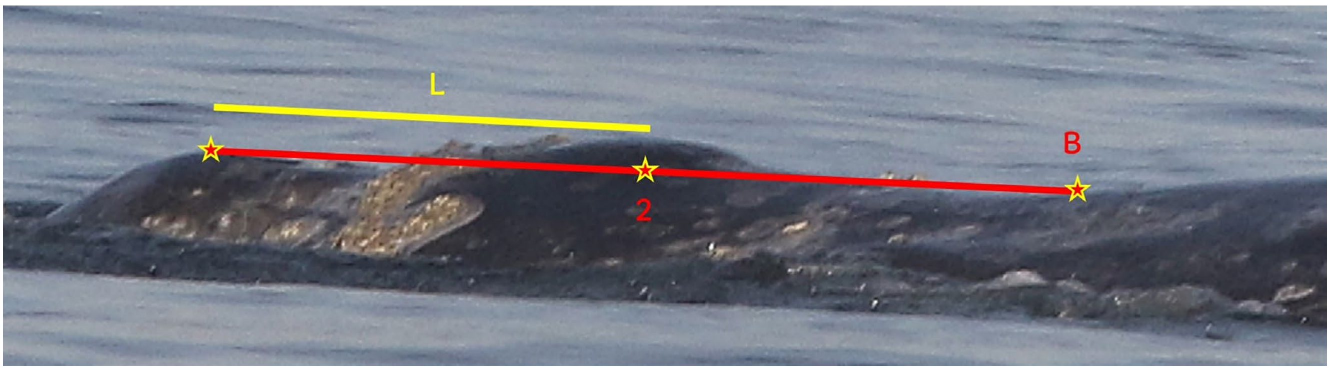

FIGURE 1 | Example image depicting the standardizing measurement. In yellow, L represents the measurement from the blowhole to the top of the post-cranial hump. In red, 2 L represents the doubled length of L to obtain the location of the anchor point for the angle measurement, B. Offset angle of this image was scored as a 1. Photo taken by Cascadia Research Collective.

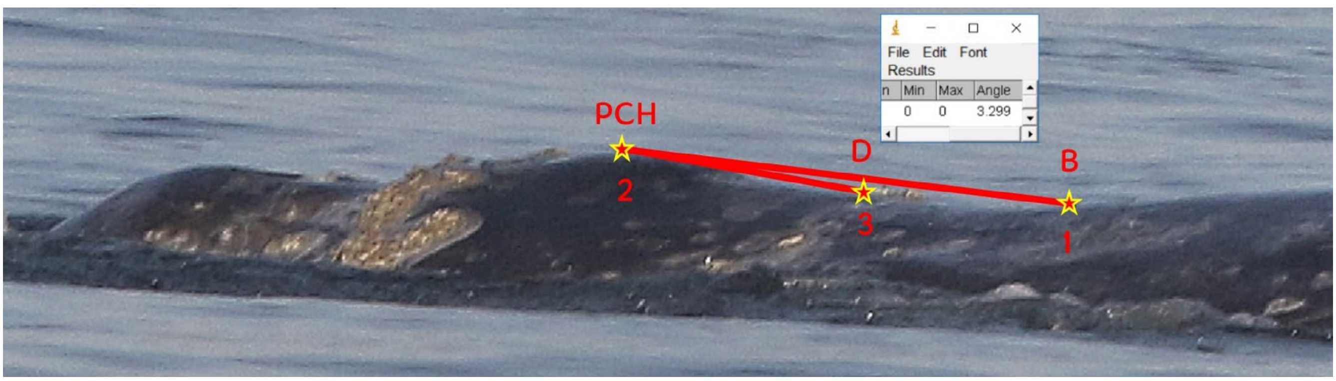

FIGURE 2 | Example image depicting the angle measurement, °*BC* (Figure 1). Point 1 (B) is the previously found anchor point along the back. Point 2 (PCH) is the top of the post-cranial hump. Point 3 (D) is the lowest point of the depression. Following placement of the points, an angle measurement can be taken. Photo taken by Cascadia Research Collective.

the lme4 package in R (Bates et al. 2015). Model selection was based on the residual maximum likelihood (REML) with the most efficient model having the smallest REML. Linear mixed models were run with two separate datasets to determine and reduce the effect of offset angle on °BC. The first dataset included all 729 photos selected for °BC measurement. The second dataset contained a subset of 559 photos in which the offset angle was < 3.

A third linear mixed model was developed to examine the relationship between time spent in Puget Sound and body condition. In this analysis, the total change in °BC for a single individual during a season spent in Puget Sound was modeled as a function of the number of days between the first and last observation of that individual over the season.

All °BC measurements used in the previously described models were conducted by a single analyst. A second analyst conducted measurements on the same set of photos to determine analyst bias in °BC measurement. A Pearson correlation was conducted between °BC measurements for a given photo measured by each analyst to quantify inter-researcher correlation.

The °BC methodology was validated against two alternative methods for assessing body condition: the Bradford method index and a drone-based measurement. Each °BC measurement photo also received a Bradford score of the post-cranial hump for comparison, where a Bradford score of 1, 2, or 3 indicates poor, average, and above-average body condition, respectively (Bradford et al. 2012). An alternative body condition index was also calculated from vertical drone images collected during the same March to June period as boat-based images in 2020. Aerial images were collected using an octocopter drone flown non-invasively at a typical altitude of 40–60 m, using methods described in Durban, Fearnbach, et al. (2015), Durban, Weller, et al. (2015), and Durban et al. (2022), except the vertically gimballed camera was a full-frame Sony Alpha A7R camera (7360 × 4912 pixels). The camera was equipped with a 55 mm F1.8 Sony lens to ensure no wide-angle distortion of images. The drone Body Condition Index (BCI) was calculated as the body width in pixels at a point 50% of the total length (TL) of the whale, represented as a proportion of the TL in pixels (e.g., Durban et al. 2016) (Figure 3). Width at 50% of TL has previously been used to quantify body condition for gray whales (Stewart et al. 2023). The BCI and *°BC* were tested with a Spearman's Rank Correlation (unpublished data, Fearnbach et al. 2020). To be included in the comparison, there had to be a *°BC* measurement within ± 7 days from the date of the drone BCI score to minimize the effect of seasonal changes in an individual's blubber thickness.

The effects of flexion throughout the dive sequence on *°BC* measurements were analyzed through the construction of a mixed effects model using the lme4 R package (Bates et al. 2015). This model included both dive sequence stage and offset angles as random variables, as well as their interaction. An ANOVA was also conducted using data from the most sighted individual between April 14, 2023, and April 17, 2023 (ID CRC-2249) to further analyze variation in *°BC* between stages and offset angles. Only images with an offset angle of 0, 1, or 2 were collected for this analysis. The results of this ANOVA were then used to conduct a Tukey HSD test to compare offset angles individually.

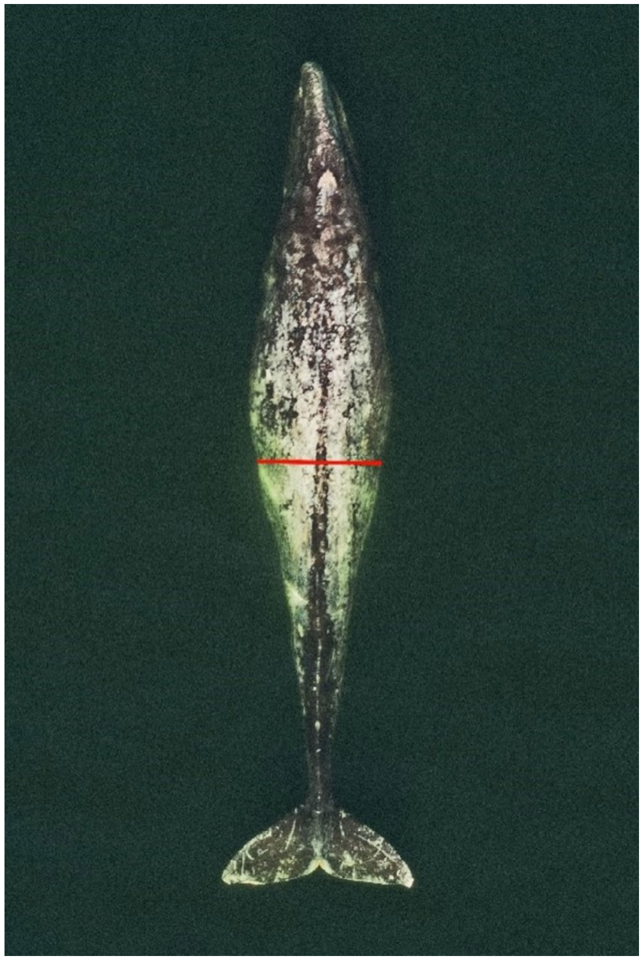

FIGURE 3 | Aerial image of a Sounder gray whale showing the photogrammetric breadth measurement at 50% (red line) which has been shown to be a variable measurement site for gray whales (Stewart et al. 2023). Image was collected non-invasively using an octocopter drone flown at > 150 ft. over the whales under NMFS research permit 22,306. Photo by John Durban and Holly Fearnbach (SR3).

3 | Results

For the 31-year study period, a database of roughly 35,000 images was queried to identify 729 boat-based photographs that were appropriate for *°BC* measurements. From these 729 images, a subset of 559 images met the criteria where offset angle < 3 (Table 1). Six of the individual Sounders were sighted frequently, with >50 photos for each of those individuals selected for °BC measurement (Table 2). The remaining five individuals were less commonly sighted, with the number of °BC measurements from selected photos ranging from 5 to 35 photos per individual. Systematic sighting effort increased over the years as research and public interest in the Sounders' aggregation expanded, and this is reflected in the total measurements per year (Table 1). Encounters were spread between the months of February (10 measurements) and June (Bradford et al. 2012), with the majority of encounters in March (236) and April (332) followed by May (144). The *°BC* measurement

TABLE 1 | Counts of measurements used in the assessment of eastern gray whale body condition by year that the photo was collected (row) and individual gray whale ID (column).

Year\ID	21	22	44	49	53	56	185	356	383	531	723	Total
2021	6	0	3	0	5	2	0	1	8	2	4	31
2020	3	13	5	6	6	2	0	1	6	4	3	49
2019	4	15	0	8	9	4	5	2	12	2	0	61
2018	9	8	5	14	9	4	0	0	12	8	7	76
2017	4	14	0	5	5	1	0	0	10	0	3	42
2016	3	0	2	2	0	1	0	0	8	6	13	35
2015	4	12	5	3	4	1	0	0	8	0	4	41
2014	0	0	1	3	3	2	0	3	5	0	6	23
2013	5	8	0	1	7	7	0	0	4	1	4	37
2012	3	4	0	1	4	0	0	0	3	0	3	18
2011	0	0	1	1	12	4	0	0	2	1	6	27
2010	2	9	1	5	3	0	0	4	3	2	0	29
2009	5	1	3	6	2	0	0	0	5	0	2	24
2008	2	3	0	3	0	1	0	0	0	1	0	10
2007	1	0	0	0	0	0	0	0	1	1	0	3
2006	3	10	0	0	4	5	0	0	2	1	4	29
2005	0	1	0	0	1	0	0	0	0	0	0	2
2004	1	0	2	0	0	0	0	0	2	0	4	9
2003	0	0	0	0	0	0	0	0	0	0	0	0
2002	0	0	0	1	0	0	0	0	0	0	0	1
2000	0	0	0	0	0	1	0	0	0	0	0	1
1998	0	1	0	1	0	0	0	0	0	0	0	2
1992	1	0	2	0	0	0	0	0	0	0	0	3
1991	2	0	0	0	1	0	0	0	0	0	0	3
1990	1	2	0	0	0	0	0	0	0	0	0	3
Total	59	101	30	60	75	35	5	11	91	29	63	559

ranged from $<0°$ for individuals with the thickest blubber layer to $>8°$ for the thinnest animals. The overall mean °*BC* measurement across all individuals and all photos was 2.071° (sd = 1.112), with a median °*BC* of 1.941°. The majority of °*BC* outliers consisted of measurements that reflect extremely poor body conditions (e.g., °*BC* > 4°) (Figure 4).

The impact of flexion during the dive sequence was assessed using 352 images collected during 2023. The resulting mixed effects model failed to show that the degree of flexion, characterized by the dive sequence stage, had a significant effect on the measurement of the °*BC*. Offset angle, however, did have a significant effect on the °*BC* measurement (Figure 5, Table 3). The ANOVA comparing stages and offset angles for ID CRC-2249 also failed to show significant variation between dive sequence stages; however, there was significant variation between offset angles (Table 4). The Tukey HSD test showed that there was significant variation between each of the three offset angles present in this dataset.

The results of the mixed effects analysis on the 1990–2021 Sounder time series showed significant, negative, relationships between °*BC* and day-of-year. Since °*BC* is inversely proportional to blubber thickness (thinner animals will have deeper post-cranial depressions), this pattern indicates that body condition generally improves as the season progresses (Table 2). The most parsimonious model for the mixed effects analysis for both datasets included all three random effects: year, ID, and offset angle, and was thus used for analyses. Variance among the random effects in dataset 1 (using the full range of offset angles) was primarily explained by offset and ID. For dataset 2, which removed measurements where the animal had an offset

TABLE 2 | Results of the mixed effects models to test the effect of Julian day (fixed) and random effects on the °*BC* using two, progressively more restrictive, datasets. The third dataset examined the relationship between time spent in Puget Sound and how much an individual's °*BC* changed from initial to final sighting.

			Fixed effects				Random effects	
Response Variable	**Dataset**		**Estimate**	**SE**	***t*-value**	**Correlation**	**Variance**	**SD**
°*BC*	Data 1—All measurements (REML:1841.3)	Intercept	3.327	0.322	10.338			
		Julian Day	−0.0138	0.00174	−7.971	−0.524		
		Year					0.0417	0.204
		ID					0.187	0.433
		Offset					0.368	0.607
		Residual					0.809	0.899
°*BC*	Data 2—Offset < 3 (REML:1430.6)	Intercept	2.271	0.238	11.427			
		Julian Day	−0.0136	0.00178	−7.656	−0.722		
		Year					0.0271	0.165
		ID					0.22	0.469
		Offset					0.0087	0.0933
		Residual					0.69	0.831
Difference in °*BC*	Data 3—Offset < 3	Intercept	−0.0278	0.12	−0.232			
		Days in sound	−0.0184	0.00366	−5.037	−0.64		
		Year					0.0662	0.257
		ID					0	0
		Residual					0.579	0.761

< 3, variance explained by the offset angle decreased considerably, and most of the variance among the random effects in this model was explained by individual ID. In this model, the correlation between °*BC* and day-of-year was stronger than in the model for dataset 1 (Table 2).

A third mixed effects model examined the relationship between days spent in Puget Sound and that individual animal's observed change in °*BC* over the season (Table 2). The days spent in Puget Sound had a strong, negative relationship with °*BC* (correlation of −0.64), indicating that the more time an animal spent in Puget Sound, the greater the improvement in body condition. Offset angle was not included as a random effect in this model because the difference in °*BC* was calculated from two different photographs: the first and last photographs of that individual within a given year.

After plotting seasonal trends using all °*BC* measurements, both observations and model predictions demonstrate a decline in °*BC* measurements with day of the year, an indicator of individual animals' improvements in body condition throughout their foraging season in Puget Sound (Figure 6). Across all years, individuals, and offset angles < 3 included in this study, there is a decreasing trend in °*BC* as the foraging season progresses, indicating successful feeding within Puget Sound (Figure 7). Individual CRC-22 is the most photographed Sounder with 101 photos included in this study, and this individual's photographic history shows a consistent trend in improving body condition throughout each season (Figure 8).

Figure 9 shows the difference between the first and last °*BC* measurement of a season as a function of the number of days between those measurements. The relationship between observed time spent foraging in Puget Sound and change in °*BC* mirrors the trends found in previous models. Most individuals show a greater decrease in °*BC* (thus a greater improvement in body condition) when more time is spent in Puget Sound, with some years as exceptions (2008, 2010, 2018, and 2019).

The Pearson correlation between analyst measurements for °*BC* was 0.727 with a *p* value < 2.2E-16. To validate the methodology, °*BC* measurements were compared to both the post-cranial hump measurement of the Bradford method scoring system (Bradford et al. 2012, Figure 10) and the drone BCI method (Durban et al. 2016, Figure 11). The majority of °*BC* measurements from this study were classified as a 2 under the Bradford method, but with good agreement between the lower °*BC* measurements and 3 s, indicating that the methods agree in classifying a whale with average vs. good body condition (Figure 10). Very few photos were assigned a Bradford index of 1 (indicative of poor body condition), indicating that °*BC* measurements can show a wider range of variation than the 3-point Bradford scale.

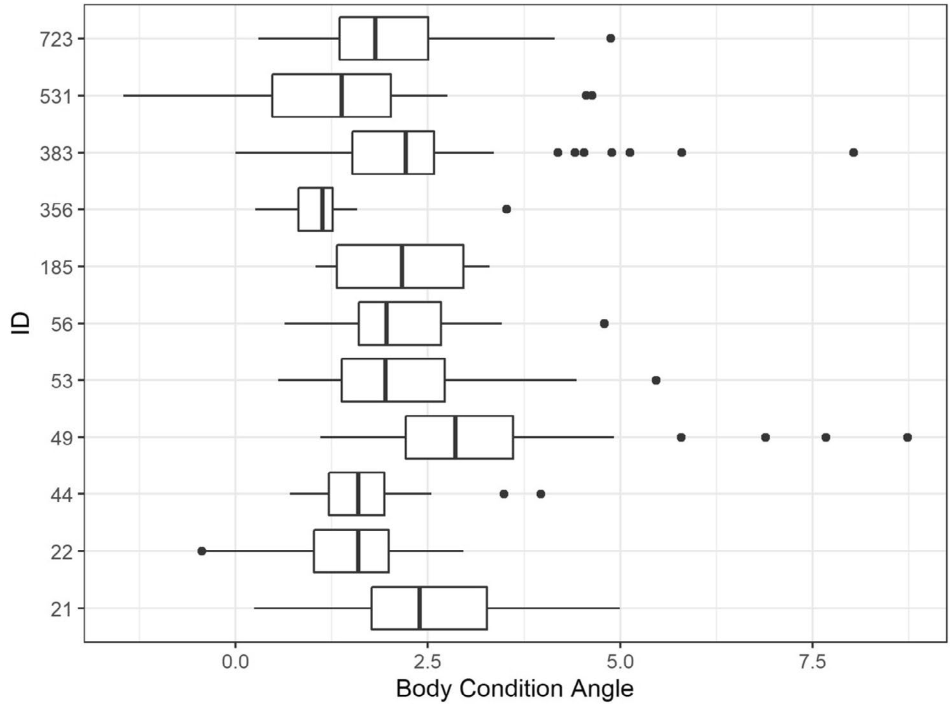

FIGURE 4 | Distribution of all °*BC* measurements for each individual over the entire sighting period. Lower and upper quartiles (creating the interquartile range; IQR) are represented by the ends of the box plots, the median is represented by the vertical line in the box plot, and outliers are represented by the dots on either side of the whiskers. Outlier points are values that exceed the range of the whiskers: Q1-1.5*IQR and Q3 + 1.5*IQR.

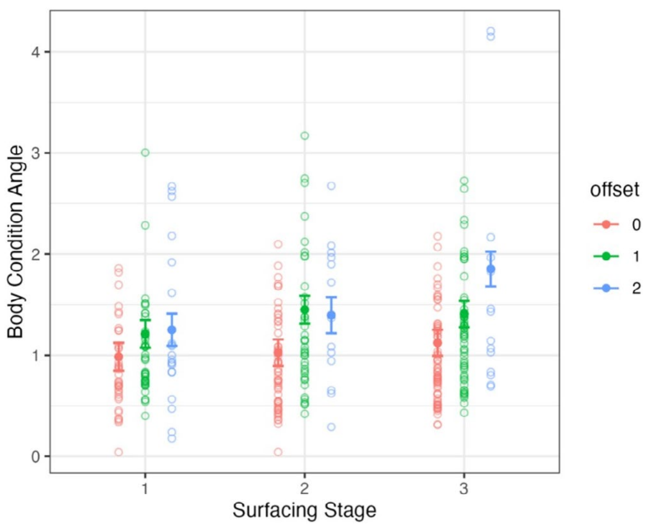

FIGURE 5 | Plot of body condition angles by surfacing event stage for the entire sample population. Open circles represent raw data points, while solid points represent predictions with error bars generated by the flexion mixed effect model (Table 3). Red points represent photos with an offset angle of 0, green points represent photos with an offset angle of 1, and blue points represent photos with an offset angle of 2.

A total of 11 pairs of drone-based BCI scores and °*BC* were available for comparison, with only 2 of the BCI scores measured on a different day than the °*BC*, but within ±7 days. The Spearman's rank correlation for the comparison of drone-based BCI to °*BC* is −0.664 with a *p* value of 0.0309. As an individual's body condition improves, drone BCI increases, and °*BC* decreases; thus the negative relationship in these indexes is appropriate. With only 11 pairs of measurements available for this analysis, the statistical power in the correlation analysis is low; thus with outliers considered, this relationship indicates a strong agreement between the measurements in these two methodologies.

4 | Discussion

Photogrammetry with drones has recently, and increasingly, been shown to offer a powerful approach to quantifying body condition of whales from aerial photographs (Christiansen et al. 2020; Durban et al. 2016; Durban et al. 2022; Fearnbach et al. 2020), particularly when condition over time can be monitored for the same individuals (Stewart et al. 2021). However, boat-based photographic records exist for a number of whale species, that extend for decades before the developments in drone photogrammetry (e.g., Pirotta et al. 2023). To assess long-term changes in condition, and relate this to changes in the environment, there is value in gleaning objective and quantitative data on body condition from such valuable long-term historical datasets.

Gray whales in Puget Sound have been studied using boat-based photo-identification since 1990 by Cascadia Research Collective (Calambokidis et al. 2002; Calambokidis et al. 2010). In this study, we used this large dataset of photographs collected over 31 years (1990–2021) to present a novel approach to assessing gray whale body condition using boat-based photographs. This method offers an innovative way to gather quantitative body condition information from historical photographic ID datasets and creates opportunities for future improvements and developments in body condition

TABLE 3 | Results of the flexion mixed effect model, which includes only offset angle, surfacing event stage, and interaction between offset angle and surfacing event stage as fixed variables and ID as a random variable.

Fixed effects						Random effects	
	Value	**Standard Error**	**df**	***t*-value**	***p***	**Variance**	**Standard deviation**
(Intercept)	1.0251232	0.1303329	334	7.865419	0.0000*	0.1222	0.3495
Offset 1	0.4254937	0.10369263	334	4.103413	0.0001*		
Offset 2	0.3714370	0.15651086	334	2.373235	0.0182*		
Stage 1	−0.040918	0.10682025	334	−0.38306	0.7019		
Stage 3	0.0974257	0.9080886	334	0.072865	0.2841	0.2443	0.4942
Offset 1: Stage 1	−0.200223	0.15336085	334	−1.30557	0.1926		
Offset 2: Stage 1	−0.103656	0.20660828	334	−0.50170	0.6162		
Offset 1: Stage 3	−0.140836	0.13600770	334	−1.03550	0.3012		
Offset 2: Stage 3	0.3593181	0.20978778	334	1.712769	0.0877		

Note: Significant *p* values are denoted using an asterisk (*).

TABLE 4 | Results of ANOVA comparing body condition angle measurements between surfacing event stages and offset angles for ID 2249, as well as results of Tukey HSD test comparing body condition angle measurements between different offset angles for ID 2249.

ANOVA results			
	df	**F**	***p***
Stage	1	3.635	0.0596
Offset	1	45.758	1.13×10^{-9}

Tukey HSD results	
Offset comparison	***p***
1–0	0.00002
2–0	0.0000004
2–1	0.0027

assessments. Specifically, this method was created using an angle tool with standardized points corresponding to an individual's anatomy, applied to digital images to generate quantitative measurements across time and uniquely identified individuals to find °*BC*. By measuring body condition as a continuous variable, this method is sensitive enough to demonstrate variations within and between seasons that may have been obscured with a more coarse, categorical body condition index (e.g., Bradford method).

Through the use of this assessment, °*BC* demonstrates utility in tracking changes in body condition within an individual's foraging season (Figures 6 and 8). Selecting photographs with an appropriately high-quality image was a limiting factor in this study as photographs needed to capture the animal nearly parallel to the boat, with a clear body outline.

As has been found with previous cetacean research, consistent access to feeding grounds with abundant high-quality prey can increase the body condition of individuals in a population (e.g., Lockyer 1987; Rice and Wolman 1971). The time spent in Puget Sound by the Sounders reflects the significance of visiting this key foraging ground for this aggregation of gray whales to build their energy reserves (e.g., Figure 8). The Sounders travel approximately 200 km off their usual migration route to forage in Puget Sound and consistently devote the extra energy and time over the last 31 years to travel to this foraging ground likely indicating successful foraging opportunities.

By examining the relationship between the amount of time spent foraging in Puget Sound and individual changes in °*BC* (Figure 9), some years demonstrated a larger improvement in body condition, given the more time spent in Puget Sound. However, there is evidence of potentially poor foraging success in 2018, when the trend was reversed and the body condition of several whales declined with increased time spent in Puget Sound. In particular, three individuals left the sound after more than a month spent there, and left with a body condition considerably worse than when they entered. All three individuals had a °*BC* more than 1° higher than the average body condition for 2018 at the time they left the sound. Two of these individuals exhibited an approximately 1.5° decrease in body condition over a 2-month period, suggesting very poor foraging success.

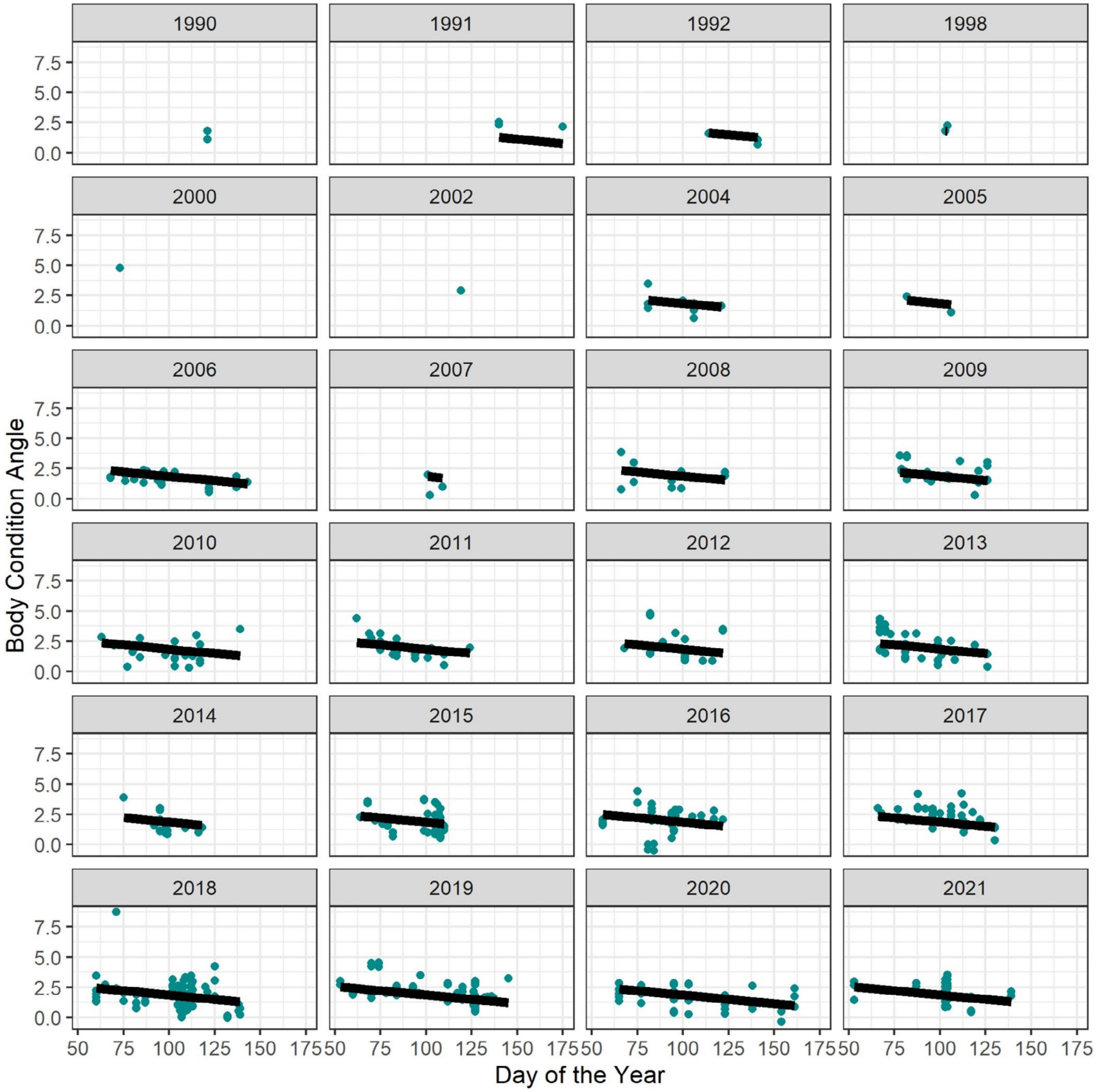

FIGURE 6 | Observations (gray points) and mixed effects model prediction (black line) of °*BC* measurement as a function of day of the year from photos scored with an offset angle < 3. Each panel represents observations and predictions for a given study year, but data are accumulated across all individuals included in this study.

This is the year preceding the start of the most recent eastern North Pacific gray whale UME, during which the majority of associated stranded whales were found to be in poor body condition, suggesting poor foraging opportunities leading to emaciation in many individuals (Christiansen et al. 2021; Stewart et al. 2023). The Eastern population likely reached the carrying capacity of its foraging grounds when its population peaked at nearly 27,000 in 2016, but has since fallen to 14,500 in the 2022/23 winter season (Eguchi et al. 2023; Stewart et al. 2023). With a larger dataset, the mixed effects model could assess interactions between year and day-of-year to quantitatively identify more and less successful foraging periods.

Ghost shrimp, the primary prey in this region for this group of whales, is an energetically valuable food source that provides 2–15 times higher biomass than any other prey for the eastern North Pacific gray whale population (Weitkamp et al. 1992). Gray whales take advantage of high tide to feed along the shallow mudflats where ghost shrimp burrow. In a method called suction feeding, the whales lay along their side and suck in a large mass of mud and biomass which they strain through their baleen plates (Johnson and Berta 2011). The °*BC* provides evidence of success in this unique foraging strategy, as demonstrated by individual trends in increasing blubber thickness with increased time spent in Puget Sound

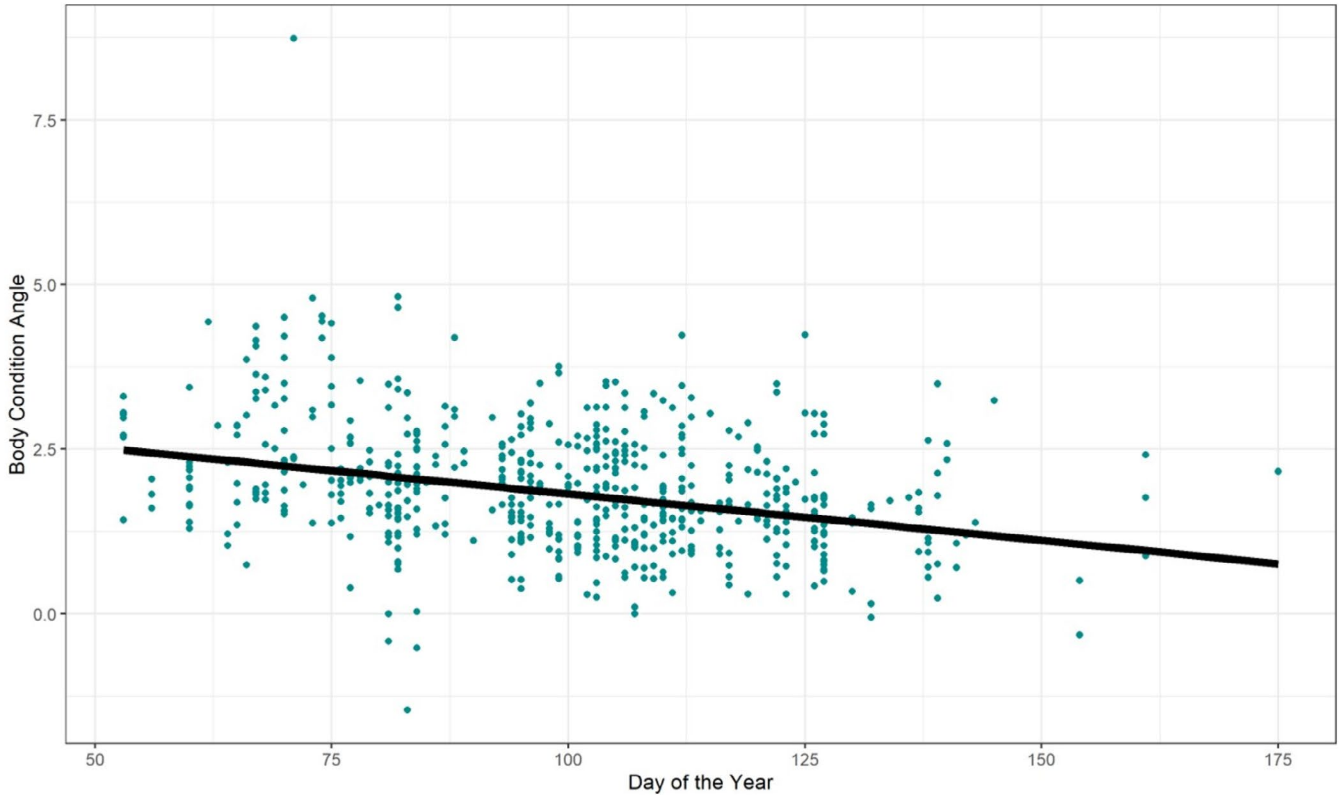

FIGURE 7 | Observations (gray points) and mixed effects model prediction (black line) of °*BC* measurement as a function of day of the year from photos scored with an offset angle < 3. Data are accumulated across all years and individuals included in this study.

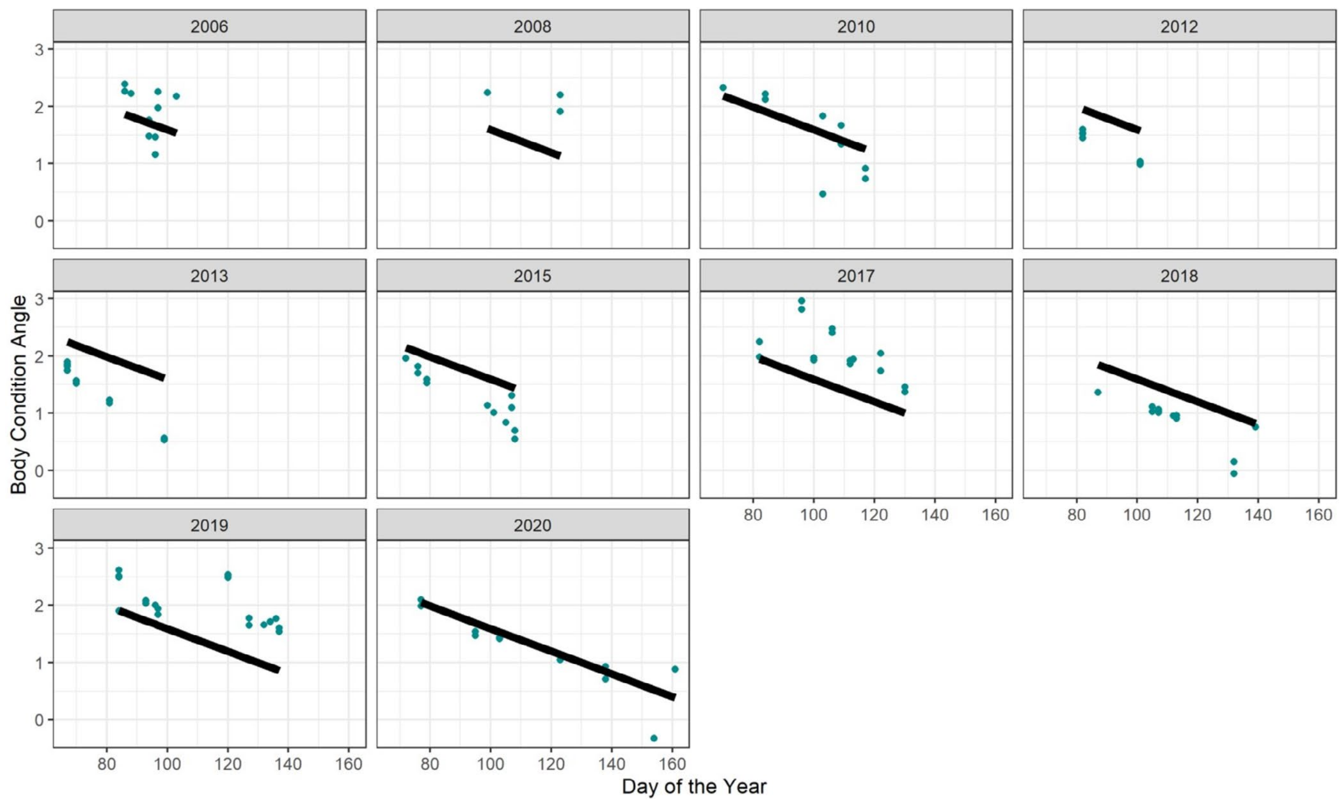

FIGURE 8 | Observations (gray points) and mixed effects model prediction (black line) of °*BC* measurement for individual #22 as a function of day of the year from photos scored with an offset angle < 3. Each panel represents observations and predictions for a given study year, excluding years that did not have any sighting data or only had a single measurement for that individual.

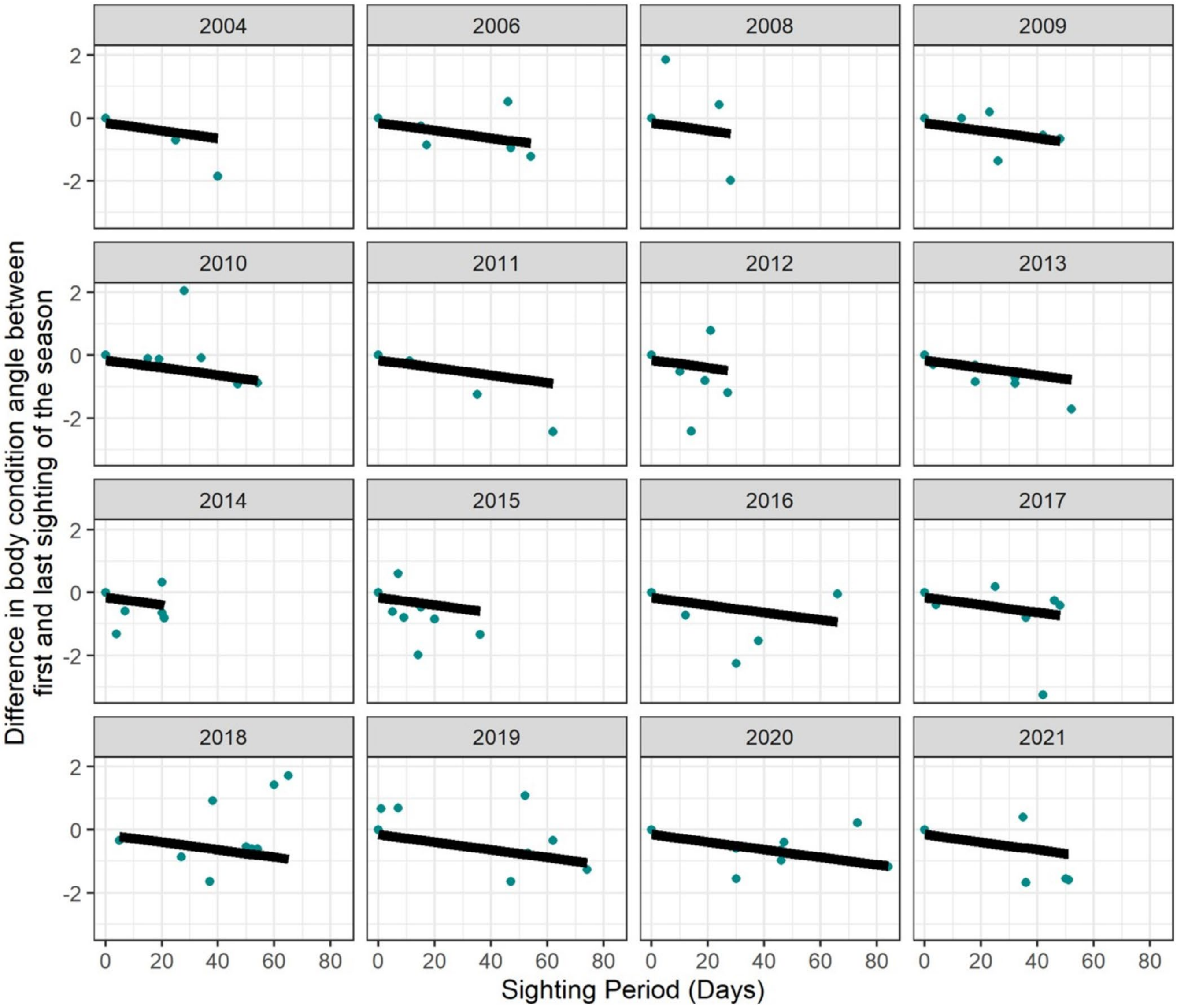

FIGURE 9 | Observations (gray points) and mixed effects model predictions (black lines) showing the relationship between number of days spent in Puget Sound and change in *°BC* for an individual animal within a single observation year. Observations and model predictions represent photos with offset angle < 3. Years with less than 4 individual animal observation periods were removed.

(Figure 9). However, not every individual experienced success every season, perhaps as a result of low available prey biomass or competition with other ghost shrimp predators. Further research to characterize ghost shrimp availability in this habitat may be useful to explain the patterns in individual and seasonal blubber accumulation measured with this body condition method.

It should be noted that this novel body condition method has only been tested on a small sample of 11 individual gray whales. Additionally, the observation location was constrained to Puget Sound, a unique foraging location for gray whales. Expansion of this body condition assessment to more individuals and locations along the migration corridor could provide more detailed explorations of fluctuations in the eastern North Pacific gray whale population's health. By applying this new body condition measurement to existing datasets for a larger eastern North gray whale subpopulation, such as the PCFG, researchers may gain more insight into the fine-scale variations in body condition between different structural groups and feeding habitats. Large historic photo databases also exist for other species of mysticetes, providing the potential for the application of this method to examine how the body condition of individuals within a population changes over longer periods. The benefit of having many photos of the same individual over a long time series is the ability to observe repeated trends in body condition changes over the time spent in foraging grounds.

While this method provides a new development to previous boat-based body condition assessments, such as the Bradford method, the complex nature of the measurement comes with challenges. There is some variation in *°BC* that cannot be fully accounted for due to changes in the angle between the observer and the animal, such as the factor described as the offset angle. Developing a quantitative method, such as a standardized angle

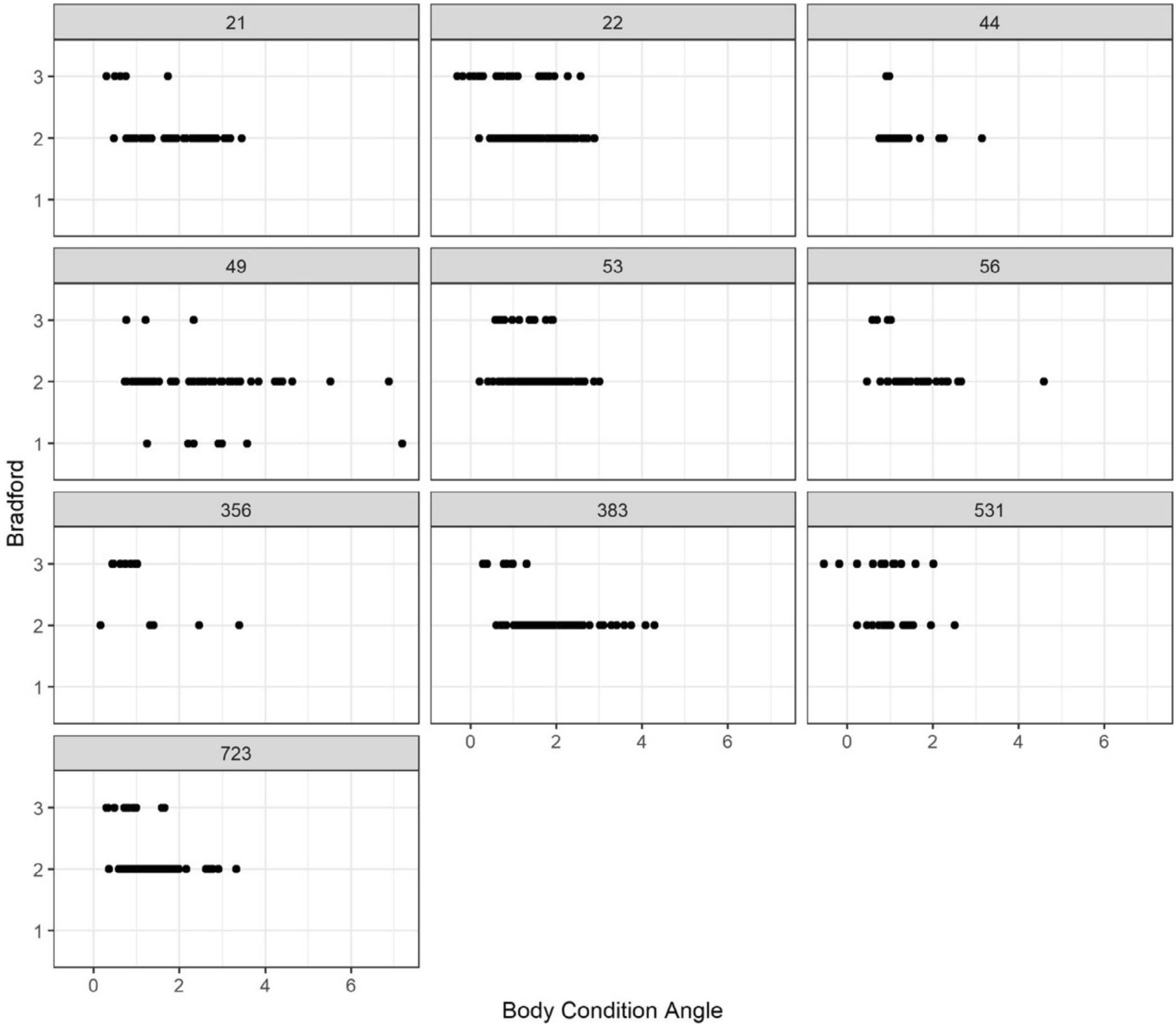

FIGURE 10 | Comparison of all °*BC* measurements (x axis) against the Bradford scoring system (y axis). Bradford scores: 1 = significant postcranial depression and hump, 2 = moderate or slight postcranial depression, 3 = flat or rounded back.

measurement, to determine the offset would likely reduce the noise in the data and allow for a more objective analysis. Alternatively, it could be beneficial when using this method to only include photos with an offset angle of 0° in order to minimize variation between measurements. Whereas the flexion variable based on surfacing event stage, however, was found to be insignificant in its effect on °*BC* measurements and therefore does not need to be considered when selecting and measuring photos. Other factors, such as variations in environmental conditions like sea state, may also create bias in the °*BC*. With these factors in mind, there is room for improvement as this method shows consistent trends in seasonal increases in °*BC* in distinct years, but noise in measurements may be reduced through more rigorous image selection parameters (e.g., Figure 8). Appropriate photos for °*BC* measurement should have the animal nearly parallel to the waterline to reduce the variation in body flexion during a breath sequence. Further modification of the °*BC* method to account for the potential impact of animal position and dive sequence timing may be valuable.

Additionally, this measurement relies on the accurate placement of the points that define °*BC*, which can be obscured by a number of factors. Photo quality is important; in particular, the size of the individual in the image combined with the resolution of the image. In lower quality photos, the edges of the whale become more pixelated, which makes it difficult to place precise anchor points and lines. Weather conditions also can alter the perception of the outline of the individual. Cloudy conditions may be preferable because they reduce or eliminate the sun's reflection along the animal's back, which can blur the edge. However, in cloudy conditions the whale's body tends to blend in more with the color of the water, which can also make it difficult to identify an edge. While photo quality was not categorized, discussions between analysts indicated the most disagreement between °*BC* resulted from photos of poorer quality. Furthermore, the standardized points of °*BC* rely on precise identification of an anatomical area, that is, the blow hole and the top of the post-cranial hump. While small differences in the placement of the points will alter the resulting measurement, the consistency among

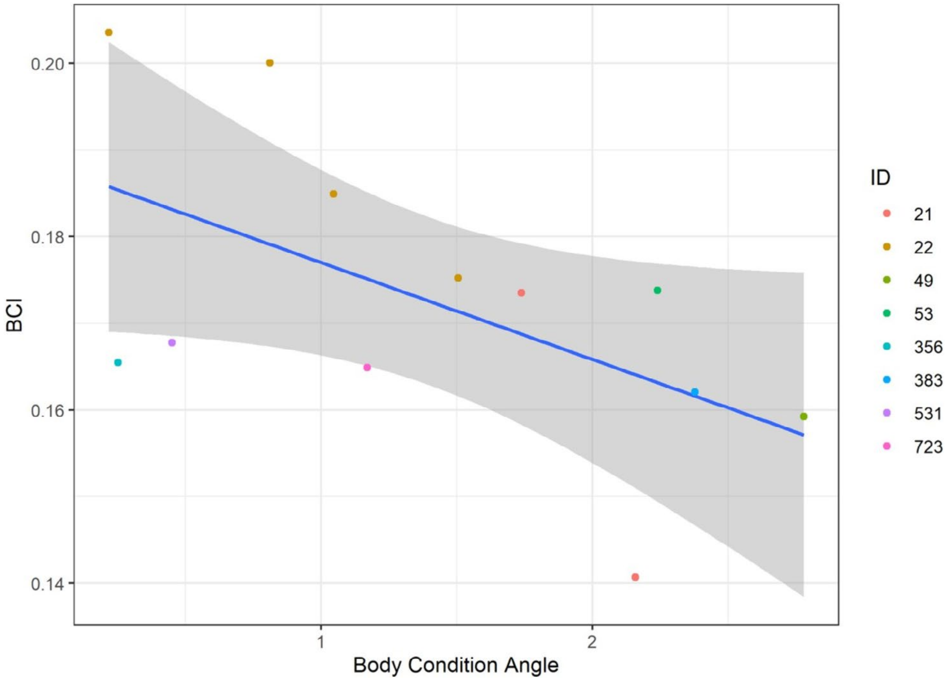

FIGURE 11 | Comparison of °*BC* measurements against the drone-based Body Condition Index (BCI) method. A linear smoother was applied. Only 11 pairs of measurements, one from each method, were available for comparison. All measurements were taken during the 2020 foraging season and the °*BC* measurements represent photos with an offset angle < 3.

seasonal trends, along with good agreement in °*BC* measurements between researchers, indicate that changes in °*BC* result from meaningful changes in the body condition of the animal. Despite the challenges inherent in photo quality and anchor point placement, sensitive and relatively objective measurements such as °*BC* can serve as a strong complement to aerial photogrammetry body condition assessments.

The development of this novel body condition index illustrates the opportunity to design more creative methods to quantitatively assess change in an individual's body condition at both seasonal and annual scales. Expansion of this method to the larger eastern North Pacific gray whale population may allow for a more detailed examination of fluctuations in body condition, likely driven by both environmental and anthropogenic impacts. There is also potential for adaptation of the method to apply to historic photo catalogs of other baleen whale species, creating opportunities for enhanced data-driven management plans.

Acknowledgments

This work was supported by University of South Carolina Magellan Scholar and Honors College grants awarded to J. Witt. Drone photogrammetry was authorized by NMFS Research Permit 19091, and supported by SR3 and the NOAA Fisheries UME Working Group.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the Cascadia Research Collective upon reasonable request.

References

Akmajian, A., J. Scordino, P. Gearin, and M. Gosho. 2021. "Body Condition of Gray Whales (*Eschrichtius robustus*) Feeding on the Pacific Coast Reflects Local and Basin-Wide Environmental Drivers." *International Whaling Commission* 22, no. 1: 87–110. https://doi.org/10.47536/jcrm.v22i1.223.

Ballance, L. T. 2018. "Contributions of Photographs to Cetacean Science." *Aquatic Mammals* 44, no. 6: 668–682. https://doi.org/10.1578/AM.44.6.2018.668.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. https://doi.org/10.18637/jss.v067.i01.

Bengtson Nash, S. M., C. A. Waugh, and M. Schlabach. 2013. "Metabolic Concentration of Lipid Soluble Organochlorine Burdens in the Blubber of Southern Hemisphere Humpback Whales Through Migration and Fasting." *Environmental Science and Technology* 47, no. 16: 9404–9413. https://doi.org/10.1021/es401441n.

Bierlich, K. C., A. Kane, L. Hildebrand, et al. 2023. "Downsized: Gray Whales Using an Alternative Foraging Ground Have Smaller Morphology." *Biology Letters* 19: 20230043. https://doi.org/10.1098/rsbl.2023.0043.

Blair, H. B., N. D. Merchant, A. S. Friedlaender, D. N. Wiley, and S. E. Parks. 2016. "Evidence for Ship Noise Impacts on Humpback Whale Foraging Behaviour." *Biology Letters* 12: 20160005. https://doi.org/10.1098/rsbl.2016.0005.

Bradford, A. L., W. D. Weller, A. E. Punt, et al. 2012. "Leaner Leviathans: Body Condition Variation in a Critically Endangered Whale Population." *Journal of Mammalogy* 93: 251–266. https://doi.org/10.1644/11-MAMM-A-091.1.

Bröker, K. C. A., G. Gailey, O. Y. Tyurneva, et al. 2020. "Site-Fidelity and Spatial Movements of Western North Pacific Gray Whales on Their Summer Range Off Sakhalin, Russia." *PLoS One* 15, no. 8: e0236649. https://doi.org/10.1371/journal.pone.0236649.

Burnham, R. E., and D. A. Duffus. 2022. "A Multi-Dimensional Examination of Foraging Habitat Use by Gray Whales Using Long

Time-Series and Acoustics Data." *Animals* 12, no. 2735: 2735. https://doi.org/10.3390/ani12202735.

Calambokidis, J., J. D. Darling, V. Deecke, et al. 2002. "Abundance, Range and Movements of a Feeding Aggregation of Gray Whales (*Eschrichtius robustus*) From California to Southeastern Alaska in 1998." *Journal of Cetacean Research and Management* 4, no. 3: 267–276. https://doi.org/10.47536/jcrm.v4i3.839.

Calambokidis, J., J. L. Laake, and A. Klimek. 2010. "Abundance and Population Structure of Seasonal Gray Whales in the Pacific Northwest 1998-2008." IWC Working Paper SC/62/BRG32, 50 pp.

Castellote, M., C. W. Clark, and M. O. Lammers. 2012. "Acoustic and Behavioural Changes by Fin Whales (*Balaenoptera physalus*) in Response to Shipping and Airgun Noise." *Biological Conservation* 147: 115–122. https://doi.org/10.1016/j.biocon.2011.12.021.

Christiansen, F., S. M. Dawson, J. W. Durban, et al. 2020. "Population Comparison of Right Whale Body Condition Reveals Poor State of the North Atlantic Right Whale." *Marine Ecology Progress Series* 640: 1–16. https://doi.org/10.3354/meps13299.

Christiansen, F., A. M. Dujon, K. R. Sprogis, J. P. Y. Arnould, and L. Bejder. 2016. "Noninvasive Unmanned Aerial Vehicle Provides Estimates of the Energetic Cost of Reproduction in Humpback Whales." *Ecosphere* 7, no. 10: e01468. https://doi.org/10.1002/ecs2.1468.

Christiansen, F., F. Rodríguez-González, S. Martínez-Aguilar, et al. 2021. "Poor Body Condition Associated With an Unusual Mortality Event in Gray Whales." *Marine Ecology Progress Series* 658: 237–252. https://doi.org/10.3354/meps13585.

Darling, J. D. 1984. "Gray Whales Off Vancouver Island, British Columbia." In *The Gray Whale Eschrichtius robustus*, edited by M. L. Jones and S. L. Swartz, 267–287. Academic Press. https://doi.org/10.1016/b978-0-08-092372-7.50018-2.

Darling, J. D., K. E. Keogh, and T. E. Steeves. 1998. "Gray Whale (*Eschrichtius robustus*) Habitat Utilization and Prey Species off Vancouver Island, B.C." *Marine Mammal Science* 14, no. 4: 692–720. https://doi.org/10.1111/j.1748-7692.1998.tb00757.x.

Durban, J. W., H. Fearnbach, L. G. Barrett-Lennard, W. L. Perryman, and D. J. Leroi. 2015. "Photogrammetry of Killer Whales Using a Small Hexacopter Launched at Sea." *Journal of Unmanned Vehicle Systems* 3, no. 3: 131–135. https://doi.org/10.1139/juvs-2015-0020.

Durban, J. W., M. J. Moore, G. Chiang, et al. 2016. "Photogrammetry of Blue Whales With an Unmanned Hexacopter." *Marine Mammal Science* 32, no. 4: 1510–1515. https://doi.org/10.1111/mms.12328.

Durban, J. W., B. L. Southall, J. Calambokidis, et al. 2022. "Integrating Remote Sensing Methods During Controlled Exposure Experiments to Quantify Group Responses of Dolphins to Navy Sonar." *Marine Pollution Bulletin* 174: 113194. https://doi.org/10.1016/j.marpolbul.2021.113194.

Durban, J. W., D. W. Weller, A. R. Lang, and W. L. Perryman. 2015. "Estimating Gray Whale Abundance From Shore-Based Counts Using a Multilevel Bayesian Model." *Journal of Cetacean Research and Management* 15, no. 1: 61–68. https://doi.org/10.47536/jcrm.v15i1.515.

Eguchi, T., A. R. Lang, and D. W. Weller. 2023. "Abundance of eastern North Pacific gray whales 2022/2023." U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-680.

Eisenmann, P., B. Fry, C. Holyoake, D. Coughran, S. Nicol, and S. Bengtson Nash. 2016. "Isotopic Evidence of a Wide Spectrum of Feeding Strategies in Southern Hemisphere Humpback Whale Baleen Records." *PLoS One* 11, no. 5: e0156698. https://doi.org/10.1371/journal.pone.0156698.

Fearnbach, H., J. W. Durban, L. G. Barrett-Lennard, D. K. Ellifrit, and K. C. Balcomb III. 2020. "Evaluating the Power of Photogrammetry for Monitoring Killer Whale Body Condition." *Marine Mammal Science* 36, no. 1: 359–364. https://doi.org/10.1111/mms.12642.

Frasier, T. R., S. M. Koroscil, B. N. White, and J. D. Darling. 2011. "Assessment of Population Substructure in Relation to Summer Feeding Ground Use in the Eastern North Pacific Gray Whale." *Endangered Species Research* 14: 39–48. https://doi.org/10.3354/esr00340.

Gendron, D., I. Martinez Serrano, A. Ugalde de la Cruz, J. Calambokidis, and B. Mate. 2015. "Long-Term Individual Sighting History Database: an Effective Tool to Monitor Satellite Tag Effects on Cetaceans." *Endangered Species Research* 26: 235–241. https://doi.org/10.3354/esr00644.

Hildebrand, L., F. A. Sullivan, R. A. Orben, S. Derville, and L. G. Torres. 2022. "Trade-Offs in Prey Quantity and Quality in Gray Whale Foraging." *Marine Ecology Progress Series* 695: 189–201. https://doi.org/10.3354/meps14115.

Ingman, K., E. Hines, P. L. F. Mazzini, R. C. Rockwood, N. Nur, and J. Jahncke. 2021. "Modeling Changes in Baleen Whale Seasonal Abundance, Timing of Migration, and Environmental Variables to Explain the Sudden Rise in Entanglements in California." *PLoS One* 16, no. 4: e0248557. https://doi.org/10.1371/journal.pone.0248557.

Joblon, M. J., M. A. Pokra, B. Morse, and C. T. Harry. 2014. "Body Condition Scoring System for Delphinids Based on Short-Beaked Common Dolphins (*Delphinus Delphis*)." *Journal of Marine Animals and Their Ecology* 7: 5–13.

Johnson, A., G. Salvador, J. Kenney, et al. 2005. "Fishing Gear Involved in Entanglements of Right and Humpback Whales." *Marine Mammal Science* 21, no. 4: 635–645. https://doi.org/10.1111/j.1748-7692.2005.tb01256.x.

Johnson, C., and A. Berta. 2011. "Comparative Anatomy and Evolutionary History of Suction Feeding in Cetaceans." *Marine Mammal Science* 27, no. 3: 493–513. https://doi.org/10.1111/j.1748-7692.2010.00420.x.

Koski, W. R., G. Gamage, A. R. Davis, T. Mathews, B. LeBlanc, and S. H. Ferguson. 2015. "Evaluation of UAS for Photographic Re-Identification of Bowhead Whales, *Balaena Mysticetus*." *Journal of Unmanned Vehicle Systems* 3: 22–29. https://doi.org/10.1139/juvs-2014-0014.

Lockyer, C. 1987. "The Relationship Between Body Fat, Food Resource and Reproductive Energy Costs in North Atlantic Fin Whales (*Balaenoptera physalus*)." *Symposia of the Zoological Society of London* 57: 343–361.

McHuron, E. A., L. Aerts, G. Gailey, et al. 2021. "Predicting the Population Consequences of Acoustic Disturbance, With Application to an Endangered Gray Whale Population." *Ecological Applications* 31, no. 8: e02440. https://doi.org/10.1002/eap.2440.

Meyer-Gutbrod, E. L., C. H. Greene, and K. T. Davies. 2018. "Marine Species Range Shifts Necessitate Advanced Policy Planning: The Case of the North Atlantic Right Whale." *Oceanography* 31, no. 2: 19–23. https://doi.org/10.5670/oceanog.2018.209.

Meyer-Gutbrod, E. L., C. H. Greene, K. T. Davies, and D. G. Johns. 2021. "Ocean Regime Shift Is Driving Collapse of the North Atlantic Right Whale Population." *Oceanography* 34, no. 3: 22–31. https://doi.org/10.5670/oceanog.2021.308.

Meyer-Gutbrod, E. L., C. H. Greene, P. J. Sullivan, and A. J. Pershing. 2015. "Climate-Associated Changes in Prey Availability Drive Reproductive Dynamics of the North Atlantic Right Whale Population." *Marine Ecology Progress Series* 535: 243–258. https://doi.org/10.3354/meps11372.

Miller, C., D. Reeb, P. Best, A. Knowlton, M. Brown, and M. Moore. 2011. "Blubber Thickness in Right Whales *Eubalaena Glacialis* and *Eubalaena australis* Related With Reproduction, Life History Status and Prey Abundance." *Marine Ecology Progress Series* 438: 267–283. https://doi.org/10.3354/meps09174.

Moore, S. E., J. T. Clarke, S. R. Okkonen, J. M. Grebmeier, C. L. Berchok, and K. M. Stafford. 2022. "Changes in Gray Whale Phenology and Distribution Related to Prey Variability and Ocean Biophysics in the Northern Bering and Eastern Chukchi Seas." *PLoS One* 17, no. 4: e0265934. https://doi.org/10.1371/journal.pone.0265934.

NOAA. 2020a. "Gray Whale (*Eschrichtius robustus*): Eastern North Pacific Stock." Marine Mammal Stock Assessment Report: 161–171.

NOAA. 2020b. Gray Whale (*Eschrichtius robustus*): Western North Pacific Stock." Marine Mammal Stock Assessment Report: 172–178.

Perryman, W., and M. Lynn. 2002. "Evaluation of Nutritive Condition and Reproductive Status of Migrating Gray Whales (*Eschrichtius robustus*) Based on Analysis of Photogrammetric Data." *Journal of Cetacean Research and Management* 4, no. 2: 155–164. https://doi.org/10.47536/jcrm.v4i2.852.

Pettis, H. M., R. M. Rolland, P. K. Hamilton, et al. 2004. "Visual Health Assessment of North Atlantic Right Whales (Eubalaena Glacialis) Using Photographs." *Canadian Journal of Zoology* 82, no. 1: 8–19. https://doi.org/10.1139/z03-207.

Pettis, H. M., R. M. Rolland, P. K. Hamilton, A. R. Knowlton, E. A. Burgess, and S. D. Kraus. 2017. "Body Condition Changes Arising From Natural Factors and Fishing Gear Entanglements in North Atlantic Right Whales *Eubalanena glacialis*." *Endangered Species Research* 32: 237–249. https://doi.org/10.3354/esr00800.

Pike, G. C. 1962. "Migration and Feeding of the Gray Whale (*Eschrichtius gibbosus*)." *Journal of the Fisheries Research Board of Canada* 19, no. 5: 815–838. https://doi.org/10.1139/f62-051.

Pirotta, E., R. S. Schick, P. K. Hamilton, et al. 2023. "Estimating the Effects of Stressors on the Health, Survival and Reproduction of a Critically Endangered, Long-Lived Species." *Oikos* 2023: e09801. https://doi.org/10.1111/oik.09801.

R Core Team. 2022. "R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing." https://www.R-project.org/.

Rice, D. W., and A. A. Wolman. 1971. *The Life History and Ecology of the Gray Whale (Eschrichtius robustus)*. Special Publication 3. American Society of Mammalogists. https://doi.org/10.5962/bhl.title.39537.

Riisager-Simonsen, C., O. Rendon, A. Galatius, M. T. Olsen, and N. Beaumont. 2020. "Using Ecosystem-Services Assessments to Determine Trade-Offs in Ecosystem-Based Management of Marine Mammals." *Conservation Biology* 34, no. 5: 1152–1164. https://doi.org/10.1111/cobi.13512.

Roger-Bennett, L., and C. A. Catton. 2019. "Marine Heat Wave and Multiple Stressors Tip Bull Kelp Forest to Sea Urchin Barrens." *Scientific Reports* 9: e15050. https://doi.org/10.1038/s41598-019-51114-y.

Saez, L., D. Lawson, and M. DeAngelis. 2021. "Large whale entanglements off the U.S. West Coast, from 1982-2017." https://doi.org/10.25923/effx-kv36.National Oceanic and Atmospheric Administration, National Marine Fisheries Service, NMFS-OPR-63A

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. "NIH Image to ImageJ: 25 Years of Image Analysis." *Nature Methods* 9, no. 7: 671–675. https://doi.org/10.1038/nmeth.2089.

Silber, G. K., D. W. Weller, R. R. Reeves, J. D. Adams, and T. J. Moore. 2021. "Co-Occurrence of Gray Whales and Vessel Traffic in the North Pacific Ocean." *Endangered Species Research* 44: 177–201. https://doi.org/10.3354/esr01093.

Soledade Lemos, L., J. D. Burnett, T. E. Chandler, J. L. Sumich, and L. G. Torres. 2020. "Intra- and Inter-Annual Variation in Gray Whale Body Condition on a Foraging Ground." *Ecosphere* 11, no. 4: e03094. https://doi.org/10.1002/ecs2.3094.

Stewart, J. D., J. W. Durban, H. Fearnbach, et al. 2021. "Survival of the Fattest: Linking Body Condition to Prey Availability and Survivorship of Killer Whales." *Ecosphere* 12, no. 8: e03660. https://doi.org/10.1002/ecs2.3660.

Stewart, J. D., T. W. Joyce, J. W. Durban, et al. 2023. "Boom-Bust Cycles in Gray Whales Associated With Dynamic and Changing Arctic Conditions." *Science* 382, no. 6667: 207–211. https://doi.org/10.1126/science.adi1847.

Stewart, J. D., and D. W. Weller. 2021. "Abundance of Eastern North Pacific Gray Whales 2019/2020. United States." https://doi.org/10.25923/bmam-pe91.National Marine Fisheries Service, Southwest Fisheries Science Center (U.S.) NOAA-TM-NMFS-SWFSC; 639

Stimmelmayr, R., and F. M. D. Gulland. 2020. "Gray Whale (*Eschrichtius Robustus*) Health and Disease: Review and Future Directions." *Frontiers in Marine Science* 7: 588820. https://doi.org/10.3389/fmars.2020.588820.

Torres, L. G., C. N. Bird, F. Rodríguez-González, et al. 2022. "Range-Wide Comparisons of Gray Whale Body Condition Reveals Contrasting Sub-Population Health Characteristics and Vulnerability to Environmental Change." *Frontiers in Marine Science* 9: e867258. https://doi.org/10.3389/fmars.2022.867258.

Valerio-Conchas, M., S. Martínez-Aguilar, S. Swartz, and J. Urban. 2022. "Gray Whale's Body Condition in Laguna San Ignacio, BCS, Mexico, for Winter Breeding Season 2022." International Whaling Commission.

von Biela, V., M. Arimitsu, J. Piatt, et al. 2019. "Extreme Reduction in Nutritional Value of a Key Forage Fish During the Pacific Marine Heatwave of 2014–2016." *Marine Ecology Progress Series* 613: 171–182. https://doi.org/10.3354/meps12891.

Wachtendock, R., J. Calambokidis, and K. Flynn. 2022. "Blue Whale Body Condition Assessed Over a 14-Year Period in the NE Pacific: Annual Variation and Connection to Measures of Ocean Productivity." *Frontiers in Marine Science* 9: e847032. https://doi.org/10.3389/fmars.2022.847032.

Ward, E. J., E. E. Holmes, and K. C. Balcomb. 2009. "Quantifying the Effects of Prey Abundance on Killer Whale Reproduction." *Journal of Applied Ecology* 46: 632–640. https://doi.org/10.1111/j.1365-2664.2009.01647.x.

Weitkamp, L. A., R. C. Wissmar, C. A. Simenstad, K. L. Fresh, and J. G. Odell. 1992. "Gray Whale Foraging on Ghost Shrimp (*Callianassa californiensis*) in Littoral Sand Flats of Puget Sound, U.S.A." *Canadian Journal of Zoology* 70: 2275–2280. https://doi.org/10.1139/z92-304.

Weller, D. W., B. Würsig, A. L. Bradford, et al. 1999. "Gray Whales (*Eschrichtius robustus*) off Sakhalin Island, Russia: Seasonal and Annual Patterns of Occurrence." *Marine Mammal Science* 15: 1208–1227.

Würsig, B., and T. A. Jefferson. 1990. "Methods of Photo-Identification for Small Cetaceans." In *Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters, Reports of the International Whaling Commission, Special Issue 12*, edited by P. S. Hammond, S. A. Mizroch, and G. P. Donovan, 43–52. The International Whaling Commission.

Young, R. A. 1976. "Fat, Energy and Mammalian Survival." *American Zoologist* 16: 699–710. https://doi.org/10.1093/icb/16.4.699.