Photogrammetry-based body condition for monitoring an Arctic marine mammal experiencing habitat loss

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ABSTRACT: Monitoring animal body condition can provide insight on population responses to environmental change. Pacific walruses *Odobenus rosmarus divergens* are experiencing loss of their sea ice habitat which has decreased the time females spend foraging during a critical period of pregnancy and lactation. Here we investigated the potential for body condition to track demographic change and be monitored via 2-dimensional aerial imagery by (1) examining whether walrus growth and body mass tracked estimated historic demographic changes, (2) collecting morphometric and body mass data and aerial imagery of walruses in human care to determine if sex, age group, and body size and condition can be determined from imagery, and (3) examining aerial imagery from a large coastal haulout used primarily by females and young to estimate potential sample sizes of measurable walruses. Body mass and growth in body length decreased between the late 1970s and early 1980s, concurrent with a period when the population approached carrying capacity and subsequently declined. Measures from aerial imagery (1) accurately distinguished reproductive-age females from subadults and adult males and (2) enabled body mass estimates with 6−7% error using either the areal footprint or a combination of length and width. We found a mean (±SD) of 216 ± 77 walruses appropriately positioned for measurement from aerial surveys of the haulout, enabling measurements of ≥7000 individuals annually via repeated daily imagery. Our results suggest that body mass of reproductive-age females and growth of dependent young may be useful indicators to augment monitoring of the Pacific walrus population and can be achieved via non-invasive aerial imagery collections.

KEY WORDS: Morphometrics · Body mass · Marine mammals · Drones · Pacific walrus · *Odobenus rosmarus divergens* · Sea ice loss

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1. INTRODUCTION

Tracking trends in large mammal populations is fundamental to species management and conservation (Di Fonzo et al. 2016) and to understanding potential changes in food webs and regional ecosystems (Lacher et al. 2019). However, estimating population size and vital rates to monitor trends is often limited by the logistics and cost of obtaining necessary sample sizes, particularly for species ranging over remote and inaccessible regions (Hammond et al. 2021). Body condition has emerged as a useful indicator of population trends (Fleishman et al. 2016, Booth et al. 2020) because of its relation to reproduction and survival of young (Keyser et al. 2005). Across a wide range of mammal species, low female body condition is associated with reduced pregnancy rates, lactation failures, and reduced size of young which contribute to lower recruitment (Guinet et al. 1998, Testa & Adams 1998, Zedrosser et al. 2013, Christiansen et al. 2016, 2018, Bright-Ross et al. 2021).

In mammals, gestation and lactation increase energetic costs for females by 17–32% and 65–215%, respectively (review by Robbins 1993, Noren et al. 2014, McHuron et al. 2023), resulting in reproduction being dependent on access to increased energy. Although some species have evolved seasonal reproductive patterns that coincide with maximum food availability (i.e. income breeders), reproductive success in most mammals requires some amount of energy reserves (i.e. capital breeding). Body condition represents energy reserves available from balancing energy intake and expenditure and therefore reflects the resources available to support reproduction and other energetic demands (Schulte-Hostedde et al. 2005, Peig & Green 2009, Schamber et al. 2009). For example, in South African fur seals *Arctocephalus pusillus*, declines in body condition resulted in higher rates of spontaneous abortions and lactation cessation (Guinet et al. 1998). Similarly, declines in female body condition of North Atlantic right whales *Eubalaena glacialis* were associated with dramatic declines in calving concurrent to a population decline over 3 decades (Rolland et al. 2016). Because of the role of female body condition in affecting reproductive outcomes and because reproductive rates are a primary driver of population dynamics (McHuron et al. 2023), monitoring body condition is recognized as a valuable tool for population monitoring and conservation of both marine and terrestrial mammals (Stevenson & Woods 2006, Moore & Huntington 2008, Fleishman et al. 2016, Booth et al. 2020).

Morphometric measures that are used to assess female body condition can also be useful for monitoring offspring size and growth, which are important determinants of their survival. A meta-analysis investigating relationships between offspring mass and survival across a wide range of mammals found that an increase in one standard deviation of body mass of offspring increased the odds of surviving by 71% (Ronget et al. 2018). Further, maternal body mass is a strong predictor of offspring mass in mammals, resulting in maternal body condition being an important factor affecting juvenile survival (Ronget et al. 2018). Thus, morphometric measures used to derive female body condition and offspring size provide a comprehensive assessment of the primary mechanistic factors affecting population recruitment (Baker & Fowler 1992, McMahon et al. 2000, Ronget et al. 2018).

Environmental changes, including those driven by global warming, often affect body condition as a result of habitat changes that alter food resources and energetics (Kovacs et al. 2011, Williams et al. 2013, Descamps et al. 2017, Boveng et al. 2020). As a result, population dynamics are primarily affected by environmental change through reproduction and survival of young rather than effects on adult survival (Moore & Huntington 2008, Udevitz et al. 2017). Similarly, density-dependent effects that result either from population growth or a decline in carrying capacity associated with habitat also affect body size and mass of mammals which impact reproduction and survival of young (Pettorelli et al. 2002, Zedrosser et al. 2006). In comparison to estimates of vital rates and population size, body condition assessments are often more feasible as a continuous, annual data source for monitoring effects of environmental change and management actions than direct, continuous estimates of vital rates and abundance (Powell & Wells 2011, Purves et al. 2013, Fleishman et al. 2016). Further, data on body condition can help identify mechanisms associated with changes in vital rates and abundance.

Pacific walruses *Odobenus rosmarus divergens* range across the continental shelves of the Bering and Chukchi Seas and currently have a population size estimated at approximately 250 000 (Beatty et al. 2022). From 1960 to approximately 1980, the Pacific walrus population is thought to have increased (Fay et al. 1989, Taylor et al. 2018) but then declined due to the combined effects of density-dependent food limitations and harvest (Fay et al. 1989, 1997). The role of food limitation is supported by multiple lines of evidence including that walruses had reduced sternal blubber thickness and had lower reproductive rates

and fewer calves in the 1980s compared to the early 1970s (Fay et al. 1989, 1997). The >30 yr decline began no later than 1981, became steepest in 1985, and then ameliorated (as harvests decreased and demographic rates rose in response to easing of density-dependent effects) until the population became stable in the 2010s (Taylor & Udevitz 2015, Taylor et al. 2018). That blubber thickness was reduced concurrent to declines in reproduction and population decline is suggestive that changes in walrus body condition could be a signal of potential population-level change.

Female walruses have an approximately 14.5 mo gestation period (Katsumata et al. 2020) and give birth to a calf in the spring (Fay 1982). Young are entirely dependent on the mother for the first year and travel with the mother, continuing to nurse into the second year (Fay 1982). Females accumulate energy reserves during gestation to support lactation demands using a mixed strategy of capital and income to meet the demands of reproduction (Noren et al. 2014). Changes to autumn foraging behavior associated with sea ice decline occur when females can be 7—9 mo pregnant or nursing a 3—5 mo old calf, a period in which energetic requirements increase by 50—101% (Noren et al. 2014). Although models have predicted that increased summer land use by female and juvenile walruses could result in declines in autumn body condition of 7—12% (Udevitz et al. 2017), no methods have been available to monitor effects of changing foraging behavior and energetics on walrus condition and calf growth. Further, recent changes in northern Bering Sea seasonal sea ice phenology and shunting of primary production from benthic to pelagic food webs (Huntington et al. 2020, Kikuchi et al. 2020) may impact the condition of females and their calves when they arrive at the haulout. Because walruses use stored energy to support lactation, declines in female body condition have the potential to affect the growth and survival of young.

Although the Pacific walrus population is thought to have been stable through at least 2015 (Taylor et al. 2018), observed behavioral responses to reductions in their sea ice habitat (Jay et al. 2017) are predicted to affect body condition via altered energetics and foraging time (Udevitz et al. 2017) and are projected to result in population decline (MacCracken et al. 2017). Walruses use sea ice for breeding, birthing, and resting between foraging bouts to the ocean floor (Fay 1982). Throughout the winter, they occupy areas of sea ice in the Bering Sea. In spring, females and juveniles follow the sea ice retreat north to occupy the Chukchi Sea throughout the summer and autumn,

while most adult males remain in the Bering Sea. Historically, females and juveniles occupied areas of high benthic biomass offshore in the Chukchi Sea by resting on sea ice between foraging bouts (Jay et al. 2012, Beatty et al. 2022). However, the Chukchi Sea has experienced some of the highest rates of sea ice loss in the Arctic (Serreze et al. 2016, Cai et al. 2021) and has been identified as one of the 3 most vulnerable marine ecosystems in the world (Kovacs et al. 2011, Albouy et al. 2020). In line with predictions of the vulnerability of the northern Pacific ecosystem, much of the Chukchi Sea continental shelf has become ice-free during the summer (Douglas 2010, Jay et al. 2012, Serreze et al. 2016), which has resulted in female and juvenile Pacific walrus coming onshore in Alaska and Chukotka to form large haulouts which can occur throughout the autumn, starting in mid-August and extending through mid-November (Jay et al. 2012, Monson et al. 2013, Goertz et al. 2017, Fischbach et al. 2022a, Fischbach & Douglas 2021). A single haulout in northwestern Alaska has been estimated to be used by nearly 190 000 walruses, representing approximately 70% of the Pacific walrus population (Beatty et al. 2022, Fischbach et al. 2022a), the majority of which are reproductive-age females, juveniles, and calves (Monson et al. 2013). Walruses using land are farther from their preferred offshore benthic foraging habitat and, as a result, spend more time traveling and less time foraging (Jay et al. 2017).

The occurrence of large, coastal haulouts of reproductive-age females, calves, and juveniles provides a unique opportunity to access Pacific walrus for monitoring the size of calves and body condition of reproductive females. Non-invasive protocols have recently been developed to monitor walrus abundance at the coastal haulout using survey drones that avoid disturbance (Fischbach et al. 2022a). Simultaneously, numerous studies have validated use of 2- and 3-dimensional imagery collected by survey drones for estimating body condition of marine mammals, including whales, seals, sea lions, and dolphins and porpoises (Waite et al. 2007, Meise et al. 2014, Christiansen et al. 2016, Fiori et al. 2017, Krause et al. 2017, Adamczak et al. 2019, Hodgson et al. 2020, Shero et al. 2021). Body condition estimated from aerial photogrammetry has been used as an indicator to monitor the consequences of disturbance and environmental change (Fleishman et al. 2016, Booth et al. 2020). These advances suggest the potential for a new, drone-based photogrammetry approach to annually monitor Pacific walrus body condition in relation to environmental variation and longer-term change.

Validation of imagery-based measurement of marine mammals hauled out on land is possible by comparing physical measurements and imagery-based measurements, and by relating imagery-based measurements to body mass and other body condition measures (Meise et al. 2014, Fiori et al. 2017). However, it is challenging to determine (1) how to monitor body condition while controlling for inherent variation in energy reserves associated with age, sex, and reproductive status (i.e. being able to remotely age and sex individuals) and (2) what metric of body condition meaningfully reflects the response of a species to environmental variation and potential effects on reproduction and survival. Animals that are continuing to grow are likely to have lower energy reserves as they expend available energy to increase size in addition to support maintenance energy requirements (Peig & Green 2009). Alternatively, reproductive-age females commonly accumulate energy reserves in preparation for reproduction and lactation (Noren et al. 2014). Thus, using body condition as a metric for monitoring the population status necessitates understanding patterns of growth and reproduction and the ability to identify cohorts based on age, sex, and reproductive status. Although body condition is often quantified as measures of body mass relative to structural size, a number of studies support that larger absolute body mass in mammals has a range of advantages (e.g. fasting endurance) that improves fitness outcomes (Wheatley et al. 2006, McHuron et al. 2023, Wishart et al. 2024). In Pacific walruses, total blubber content is closely correlated with both body mass and mass divided by length (r = 0.95 and 0.98, respectively; Noren et al. 2015), suggesting that monitoring body mass, particularly in adult females, may be a useful indicator of available energy reserves.

Here we examined the potential for walrus morphometrics to provide insight into population demographics and to validate 2-dimensional aerial imagery as a method for estimating the body mass and body condition (mass relative to length) of Pacific walrus. We chose to investigate the use of 2-dimensional (2D) rather than 3-dimensional (3D) aerial imagery because (1) body condition and 2D measures are strongly correlated (Hodgson et al. 2020); (2) body mass estimated from 2D images (Krause et al. 2017) and 3D models have similar errors of <5% (Beltran et al. 2018, Bierlich et al. 2021); and (3) 2D images may be collected from survey drones with less risk of disturbance because the survey drone may be flown in a steady manner without sharp bank turns (Meise et al. 2014). Our goal was to develop a protocol to monitor body condition of reproductive-age females and

calves. We utilized a published data set of morphological measures of free-ranging Pacific walruses harvested in the Bering and Chukchi Seas between 1972 and 1991 (Bukhtiyarov & USGS Alaska Science Center—Walrus Research Program 2024) in combination with collection of data from trained walruses in zoos and aquaria that could be imaged, directly measured, and weighed (USGS Alaska Science Center—Walrus Research Program 2024). The large body size of Pacific walruses and challenges with safe sedation in field conditions (Acquarone et al. 2014, Ølberg et al. 2017) led us to focus validation of photogrammetry for body mass and size estimation in Pacific walruses in human care whose range of body masses is similar to that of free-ranging walruses (Noren et al. 2015). Specifically, the objectives of our study were to:

(1) Assess variation in Pacific walrus somatic growth and body mass relative to estimated historical changes in population demography.

(2) Determine whether morphological measures obtained from aerial imagery can be used to monitor the body size and mass of adult, reproductively mature female walruses and dependent young.

2. MATERIALS AND METHODS

2.1. Methodological approach to address objectives

We used 3 data sets to address our objectives described in detail in subsequent sections:

(1) Body length, body mass, and age data of free-ranging Pacific walruses harvested from Soviet ships between 1972 and 1991 (Bukhtiyarov & USGS Alaska Science Center—Walrus Research Program 2024). These data were used to address Objective 1 by examining patterns in somatic growth and body mass relative to estimated demographic patterns for the population during this time (Fay et al. 1989, Taylor & Udevitz 2015, Taylor et al. 2018). In addition, these data were used to determine the age at which walruses contribute energy to increasing structural size (i.e. are still growing in size) versus ages when variation in body mass largely reflects changes in energy reserves (e.g. blubber).

(2) Morphological measures, aerial images, and body mass of walruses of both sexes over a range of ages in human care in the USA and western Europe (USGS Alaska Science Center—Walrus Research Program 2024) were collected in positions commonly observed at walrus haulouts while resting or moving. This provided a data set to address Objective 2 by investigating relationships between physical mea-

sures, imagery-based measures and body mass and to identify morphological measures that might be used to classify the sex and age of walruses based on aerial imagery. The initial investigation used data collected in a single position (resting sternally recumbent). Relationships between morphometrics and body mass were then compared to an additional position common at haulouts (head up and upper body raised while moving in sternal recumbency).

(3) Images collected from survey drones at a large, coastal haulout occupied primarily by females and young near Point Lay, Alaska, USA, in 2018 and 2019 (Fischbach et al. 2022a,b) for the purposes of estimating walrus abundance were used to estimate potential sample sizes of walruses that may be measured through annual aerial surveys.

2.2. Patterns in walrus structural size and body mass during a period of demographic change

We fitted von Bertalanffy growth curves to length and body mass data of free-ranging walruses harvested in 1972—1991 to better understand how length varies with age and potential age cut-offs that could be used to distinguish fully grown, reproductive-age males and females from those that are continuing to grow (i.e. age at which 90% of maximum size is obtained; e.g. Kingsley et al. 1988, Adamczak et al. 2023). Walruses were harvested and measured as encountered in the Bering and Chukchi Seas across all months in multiple years except January. We consider these data to be representative of the population at the time because animals were harvested opportunistically, and specific demographic groups were not targeted. Walrus age was determined from teeth cementum annuli. Data were quality-controlled as described in Text S1 in the Supplement at www.int-res.com/articles/suppl/m751p211_supp.pdf. We used length data for males and females between 1972 and 1991 but restricted body mass data in growth curves of females to the months of August—October, which had the largest seasonal sample size, due to substantial seasonal variation that could be associated with reproduction. Although males may exhibit some seasonal variation in body mass during breeding, monthly variation in body mass did not follow a clear pattern with breeding behavior, so we used all available data for males. From the growth curve equations, we calculated and report the age at which males and females reached 90% of maximum length and body mass since many species continue to increase in lean body mass even after structural growth has largely ceased (Kingsley et al. 1988, Swenson et al. 2007). Length of free-ranging walruses was recorded as zoological length (the length of a walrus from nose to tail along the body contour in sternal recumbency). Although this length measure is not directly comparable to the straight-line length measures that can be collected from imagery (see Section 2.3), growth curves with zoological length still identify the age at which females reach the majority of their structural size.

We examined annual variation in mean structural size, based on body length measurements, and body mass achieved by harvested free-ranging male and female walruses from available data collected in the 1970s and 1980s. We included only males and females that had reached or exceeded the age at which 90% of maximum structural size was achieved, as determined from growth curves of body length. We hypothesized that body mass and size of growing animals would increase concurrent to population increase and subsequently decline as the population approached carrying capacity sometime between 1975 and 1981 due to density-dependent food limitations. We examined body length of walruses relative to their year of birth and compared groups of years with high or low body length. Groupings of years with high or low body length were identified for comparison based on plots of annual mean body lengths and compared using a Kruskal-Wallis test with Bonferroni-corrected pairwise tests. Because groupings were made based on patterns in the data, comparisons identified whether there were significant differences among grouped years and thereby identified birth years associated with higher or lower adult body lengths. We compared body mass of males and females that had reached 90% of maximum structural size among the 3 or 4 years in which data were available which spanned the time period in which demographic change occurred (females: 1973, 1978, and 1983; males: 1976, 1980, 1981, and 1991). Because body mass data were collected during different months for different years and body mass may vary seasonally, we selected 2 consecutive months with the highest sample size for analysis (July—August for females and March—April for males). Both males and females reach maximum structural size prior to reaching maximum body mass. Therefore, we used the residuals from the growth curve of mass relative to age, to standardize all data relative to age. Comparisons were made using a Kruskal-Wallis test with Bonferroni-corrected pairwise tests. All statistical analyses were conducted in SPSS (Version 28.0.1.0, IBM).

2.3. Collection of physical measurements and imagery of walruses in aquaria and zoos

We collected morphological measurements and aerial imagery of 21 walruses (8 males, 13 females) ranging in age from 2 to 45 yr at 6 zoos and aquaria in the USA (Indianapolis Zoo, Point Defiance Zoo, SeaWorld San Diego, and SeaWorld Orlando), Belgium (Pairi Daiza), and Germany (Hagenbeck Zoo) (USGS Alaska Science Center—Walrus Research Program 2024). Research protocols were approved by the respective institutions' Animal Care and Use Committees. Three females and 1 male were measured twice 8 mo apart when their body mass was at or near their annual low and high. To simulate measurements that can be obtained from drone imagery, we physically measured 2 straight-line linear widths (behind the front flippers and at the hips, hereafter referred to as 'front flipper width' [FFwidth] and 'hip width' [Hwidth], respectively) and straight-line length (hereafter referred to as 'length') while walruses were sternally recumbent (i.e. flat on their bellies; Fig. 1). Physical measurements were made simultaneous to aerial imaging. Walruses were positioned for measurement and imagery with their bodies in a straight line, heads down or forward, and flippers to the sides and back (Figs. 1 & 2), although some minor variation occurred (e.g. a single flipper tucked, head slightly off center). Length was measured from the tip of the nose to the tip of the tail between the back flippers (Fig. 1). Either before or after imaging and collection of linear measurements, walruses were weighed and full girth behind the front flippers was measured (hereafter referred to as 'girth'). Linear measurements were collected either with a tape measure or string suspended above the body contour, by using chalk marks on the floor to identify the edges of the body, or by measuring the distance between 2 sticks held vertically at the edges of the body. Methods varied due to sensitivity of walruses to the different approaches. Girth was measured using either a fabric tape measure or string wrapped around the body of the walrus behind the front flippers.

Aerial imagery was collected using a cable-mounted remotely triggered compact camera (with a 1" [25.4 mm] complementary metal oxide semiconductor sensor and a 24–70 mm zoom ranges in 35 mm equivalent
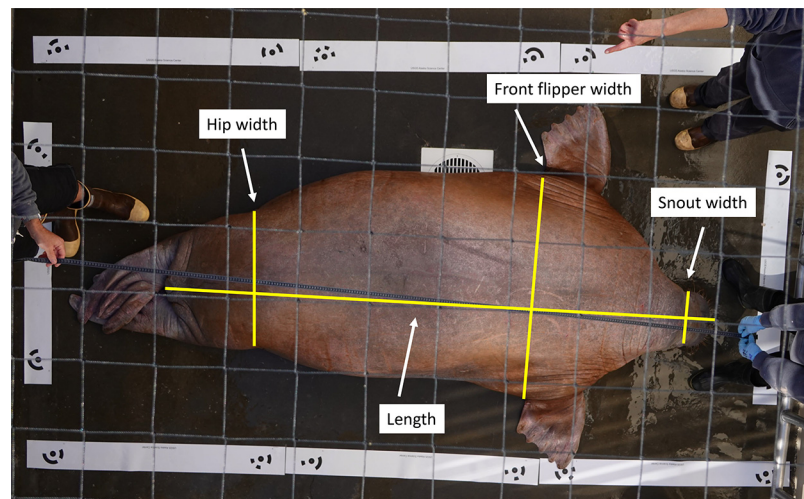

Fig. 1. Physical and image-derived measurements collected from Pacific walruses in human care at facilities in the USA and western Europe. Full girth was also collected at the same location as front flipper width. Linear measurements are indicated by yellow lines. Scale markers placed on the floor around the walrus were used to establish scale of the aerial images and quantify measurement error

Fig. 2. Adult female walrus positioned flat and resting for imaging at SeaWorld Orlando, Florida. The cable-mounted camera is visible at the top of the photo

f1.8—2.8 lens; Sony DSC-RX100 III; Fig. 2) because drone flights were not feasible at facilities where walruses were in human care. We positioned the camera 3—10 m at approximately a 90° angle to the longitudinal axis of the walrus (Meise et al. 2014) using a remotely operated camera trolley suspended from a cable (Fig. 2). We adjusted the camera to point directly downward at nadir using spirit levels and used a constant zoom setting at each facility. We placed 6 scale markers on the ground surrounding the walrus to establish scale in the images (Figs. 1 & 2). A minimum of 10 images was collected for each walrus in the trained position. Images were also collected while walruses moved into and out of position with head up and pushed up on their front flippers, to mimic a common posture observed at haulouts. These images were used to compare positional effects on body mass estimation as described below.

We selected photos that minimized shadowing and that had the best lighting to identify body edges used in measurement. A single image was measured for each walrus. Once an image was selected, the resolution of the image was resampled to 1 cm resolution to match the resolution that is common for imagery collected by drones in wildlife studies (Fiori et al. 2017). Resolution conversion was performed in Photoshop (version 24.7.3, Adobe). Examination of the 6 scale markers in each image revealed that geometric distortion was not a concern in any images.

Walrus measurements from images were collected using the ImageJ software (http://imagej.net, Schneider et al. 2012, Meise et al. 2014). A single scale marker was used to set the image scale, and imagery measurement accuracy was determined by comparing image-measured and known lengths of 3 scale markers. The same 2 linear width measurements and straight-line length measurement that were physically collected for each walrus were collected from the image. In addition, the surface area of each walrus's footprint (hereafter referred to as 'body area') was measured by manually digitizing a polygon around the walrus's body outline, excluding the hind flippers (Hodgson et al. 2020).

2.4. Comparison of physical and imagery-based measurements

We examined relationships between physical and imagery-based measurements using paired *t*-tests and Pearson correlation analysis. However, it is important to note that physical measurements are not without error (Hodgson et al. 2020). This is particularly true for the straight-line measures collected in our study to match the linear imagery-based measures. Straight-line measures have to be collected above the body contour of the walrus and therefore require a visual determination of the edge of the walrus relative to the tape measure or string, which introduces error. Although walruses are 3-dimensional, all measurements were taken at the edge of the body such that they were independent of the walrus's height. For example, straight length was the same measure whether it was taken above the walrus avoiding the body contour or taken as chalk marks noting the body edge on the substrate. As a result, the resolution of the scale marker matched the resolution of the image-based measurements.

2.5. Relationships between image-derived measurements and walrus body mass

To identify the measurements or combination of measurements from imagery that best predicted body mass, we compared a suite of multiple linear regression models that included body area and all possible combinations of Hwidth, FFwidth, and length measured from imagery as predictors (independent variables) of body mass (dependent variable). We compared models using Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002) and identified top models as those with $\Delta AIC_c \leq 2.0$. Although we sought the best predictive model for estimating body mass, rather than the most parsimonious model, we used AIC_c to aid in avoiding overfitting models. Initially, we included a random, repeated measure effect in models to account for 4 of the 21 walruses being measured and imaged more than once. If random effects were not significant, we removed the random effect and treated the multiple observations of those 4 individuals which were collected at body masses that differed between measurements by 10—100 kg as independent observations. Because footprint and body length can be metabolically scaled to body mass via a power function (e.g. Alvarado et al. 2020), we also examined models with log-transformed variables to see if they improved model fit and reduced residual error.

Because we were interested in the best predictive model for estimating walrus body mass from survey drone imagery, we allowed model variables to be collinear (Shmueli 2010). Normality was examined with a Shapiro-Wilk test, linearity was confirmed by examination of residuals, and goodness of fit was examined via a chi-squared comparison with an intercept-only model. We report estimation error as the mean resid-

ual with standard deviation (i.e. difference between observed and estimated values, per Krause et al. 2017). A set of models was examined for predicting body mass of walruses of all ages and both sexes and of adult, reproductive-age females ≥8 yr. Because we were interested in specifically being able to monitor the body condition of reproductive-age females, we examined whether body mass estimation was improved using a model specific to this sex/age class. We selected females ≥8 yr based on data indicating that female Pacific walruses ovulate by the age of 8 whereas only a portion of 6–7 yr old walruses ovulate (Fay 1982, Robeck et al. 2022) and due to patterns in morphometric growth further investigated below.

We examined potential differences in the relationships between imagery-derived morphometric measures and body mass for walruses imaged in 2 postures: the trained flat, resting posture and an upright, moving posture when walruses had their flippers more beneath their front body (Fig. 3). Although walruses at haulouts are primarily resting, the majority of resting walruses pile together such that their bodies overlap, precluding measurement. Individuals that are sufficiently separated from the herd occur primarily at the herd edges, while either moving to enter from the water or along the land edge. When moving, walruses assume a 'moving' posture, pushing up on their front flippers, which can reduce their linear width and body area. Thus, to potentially increase the sample size of walruses that can be measured at the haulout, we examined our ability to estimate body mass from images of walruses in this posture, including determining whether a separate predictive body mass relationship (Meise et al. 2014) might be used to estimate body mass for this 'moving' posture. The 2 positions are distinguishable because in a moving position the flippers are less visible because they are tucked under the front of the body whereas in the resting position almost the entire flipper is visible lateral to the body (Fig. 3). We compared length, FFwidth, and body area between the flatter, resting and more upright, moving postures using paired t-tests. We examined regressions between body area or FFwidth and length with body mass, including model fit and linearity and quantified differences in body area and FFwidth between the 2 postures.

2.6. Identifying sex, age, and reproductive classes for monitoring from aerial imagery

Although coastal haulouts that form in the Chukchi Sea in September and October are primarily attended by females, juveniles, and dependent calves, some males are also present (Monson et al. 2013). Established methods for classifying the age and sex of walruses based on frontal views were developed by Fay & Kelly (1989), who reported that proportional snout widths enabled distinction of males from females by the time males reached 6–9 yr of age. Therefore, we examined whether snout width, measured from above via aerial imagery (Fig. 1) might be used to differen-

Fig. 3. Example images comparing positions of 2 walruses when pushed up on their front flippers while moving in a more upright position (left-most image for each pair) and when resting, flat (right-most image for each pair)

tiate males and females. We compared imagery-derived snout widths between males age ≥5 and females of all ages in human care using an ANOVA. We also used a binary logistic regression with sex as the dependent variable and snout width as an independent variable to determine if snout width could be used to differentiate between males and females. Monitoring the body condition and size of calves does not require differentiating between males and females because growth parameters and total energy requirements do not differ for the first 2 yr of life (Noren et al. 2015, Katsumata et al. 2020, Robeck et al. 2022). Therefore, we did not attempt to identify a method for sexing calves via morphometric measures.

Once sex is determined for a walrus at the haulout, our next step is to differentiate reproductive age females from younger females using morphometric measures we can obtain from drone imagery. Using information from growth curves of free-ranging walruses and known age of first ovulation (Fay 1982, Robeck et al. 2022), we chose to investigate whether we could distinguish females ≥8 from females <8 yr of age from our data set of walruses in human care based on their length. We compared length between these 2 age groups using an ANOVA and used a binary regression with length as the independent variable and age group as the dependent variable.

For binary regressions identifying males and females using snout width and female age groups using body length, we used a Hosmer-Lemeshow χ^2 and p-values to determine model fit (i.e. significant differences confirm adequate fit).

2.7. Determining potential sample sizes of wild walruses at haulouts

We examined orthoimagery collected from a survey drone (1.8 kg 3DR Solo quadcopter, 3D Robotics) during 2018 and 2019 (3 each year) from 107−110 m altitude (based on a built-in barometric altimeter augmented by a Global Navigation Satellite System-enabled inertial measurement unit) at a large (used by >100 000 walruses) coastal haulout in northwestern Alaska (Fischbach et al. 2022a,b) to estimate the potential number of walruses that might be measured annually from drone surveys. This imagery had previously been collected for the purpose of estimating herd size and was not designed for photogrammetry. Therefore, we did not measure walruses from these images but rather used them to assess the sample size of walruses positioned for measurement.

Walruses were identified as measurable if their length, width, and body area were clearly visible with no overlap with other walruses and if they were either in a moving, upright position with flippers tucked under their body or a resting position with flippers out (Fig. 3). Orthoimages were generated from georeferenced images using structure from motion algorithms as described by Fischbach et al. (2022a). We annotated these orthoimages using desktop GIS software (QGIS, version 3.28.15; https://qgis.org) by placing point markers on individual walruses identified as being appropriately positioned for measurement (Fig. 4) and distinguishing females accompanied by calves (based on direct contact between the female and a calf), yearling calves, older dependents, and unknown independent walruses. Insufficient image resolution (approximately 2.1 cm pixel^{-1} with substantial motion-induced blur) precluded measurement of walruses to classify sex and age. The age of dependent calves was estimated based on their size in relation to their mother.

3. RESULTS

3.1. Variation in walrus structural size and body mass during a period of demographic change

Patterns in body length relative to birth year differed between males and females as evidenced by plotted patterns for females, in which the period of birth years associated with longer adult body lengths
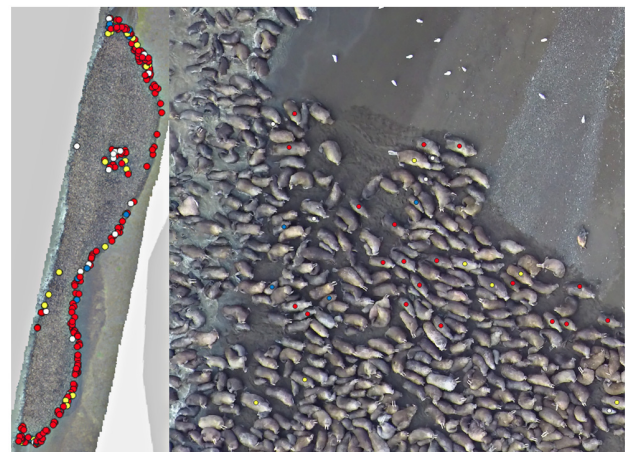

Fig. 4. Locations of walruses identified as being in an appropriate position for measurement from an orthoimage collected by survey drone 6 September 2018 at a haulout near Point Lay, Alaska. Red dots indicate lone, non-calf walruses, yellow dots indicate females with calves, white dots indicate first-year calves, and blue dots indicate calves >1 yr old

occurred later than in males (Fig. 5). Body length of wild-harvested adult female walruses was 9 and 12 cm shorter for those born 1965–1975 and 1981–1983 compared to 1976–1980, respectively (Fig. 5, groups shown as different symbols; Kruskal-Wallis test = 14.2, p < 0.001, pairwise tests with Bonferroni correction: 1965–1975 and 1976–1980 = −3.6, p = 0.001, 1976–1980 and 1981–1983 = 2.6, p = 0.03). A similar pattern was apparent for males, with those born 1971–1974 growing 13 and 7 cm longer than those born 1965–1970 and 1975–1978, respectively (Fig. 5; Kruskal-Wallis = 27.6, p < 0.001; pairwise tests: 1965–1970 < 1971–1974: −5.2, p < 0.001, 1971–1974 > 1975–1978: 2.4, p = 0.05).

Residual body mass of adult female walruses ≥8 yr harvested in July and August was 80 and 108 kg lower in 1983 than in 1973 and 1978, respectively (Fig. S1; Kruskal-Wallis test statistic = 138.6, p < 0.001, all
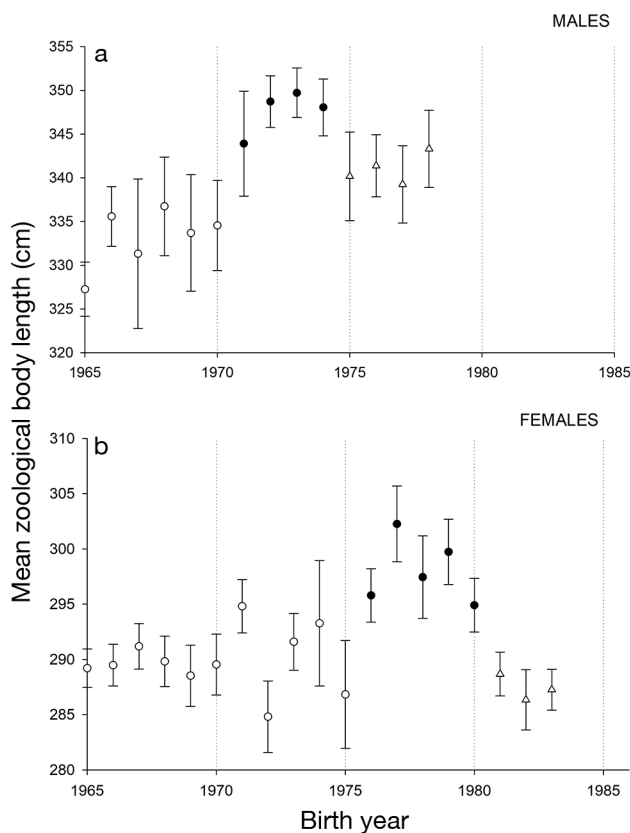
Fig. 5. Annual mean (±SE) zoological lengths of (a) male and (b) female walruses harvested during cruises in the Chukchi and Bering Seas relative to their year at birth. Walruses were grouped into 3 time periods based on consecutive high or low body lengths (different symbols) for comparison. Walruses were included that were at or above the age in which they achieved 90% of their structural size (≥8 yr for females and 13 yr for males based on von Bertalanffy growth curves in Figs. S4 & S5

pairwise tests: p < 0.001). Residual body mass did not differ between 1973 and 1978 (pairwise test = −2.3, p = 0.06). Similarly, residual body mass of adult male walruses ≥13 yr was 45 and 111 kg lower in 1981 and 1991 (which had similar residual body mass) compared to 1976 and 1980, respectively (Fig. S1, Kruskal-Wallis test statistic = 28.2, p < 0.001, all pairwise tests: p < 0.05).

3.2. Relationships between physical and imagery-derived measures

There was no difference between physical and image-derived measures of FFwidth (paired $t = −0.52$, df = 22, p = 0.61) or length ($t = −1.43$, df = 19, p = 0.17) (Fig. S2). Imagery-derived measurement of scale markers were on average within ±1.1 cm (1.0%) of the actual measure (102.5 cm). The measured FFwidth of 2 walruses were outliers (>2.5 × SD) in the relationship with image-derived measures as well as with body mass and were removed from the data set as presumed measurement or recording error. Excluding those data points, image-measured length and FFwidth (position 1 in Fig. 1) were closely correlated to physical measures (Fig. S2). Physical and image-measured FFwidth values were also closely correlated to full girth at the same location ($R^2 = 0.91$, $F_{1,15} = 143.6$, p < 0.01; Fig. S3).

3.3. Relating imagery-based measurements to body mass

Length and FFwidth were correlated with body mass (Fig. 6), but the linear model including body area had the best fit to body mass data (i.e. had the lowest AIC_c, $R^2 = 0.91$, Table S1) for 10 females and 8 males (n = 21 observations; Fig. 7). However, the residual standard error on predictions from the model containing body area was higher (±66.9 kg) than error on the model that included length and width (±57.0 kg, $R^2 = 0.93$), which also was among the top models ($\Delta AIC_c = 1.2$, Table S1). Both of these top models had a fit that was improved relative to an intercept-only model (p < 0.001) and had similar distribution of residuals. A random effect accounting for repeated measure of 4 individuals was not significant (p = 0.98), so candidate models were run as multiple linear regressions without the random effect. Data were normally distributed (Shapiro-Wilk = 0.93, df = 27, p = 0.07), and residuals indicated good fit with a linear model. Although models with transformed vari-
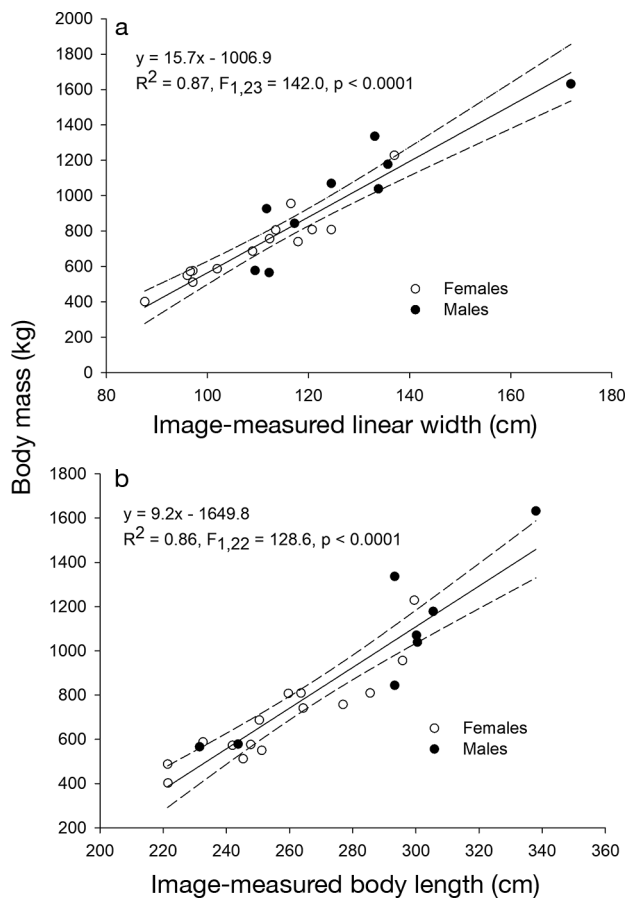
Fig. 6. Relationships between body mass and (a) image-measured linear width behind the front flippers and (b) image-measured body length of female and male Pacific walruses held in aquaria and zoos and ranging in age from 2 to 45 yr. Regressions were fit to combined male and female data. Dashed lines are 95% confidence intervals
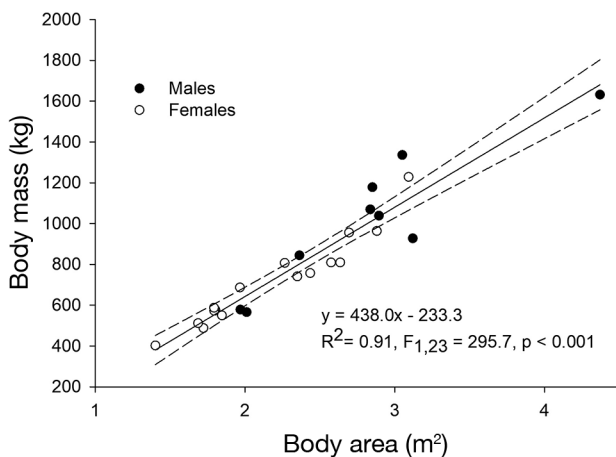

Fig. 7. Relationship between the area of the body from imagery (excluding the flippers) and body mass of female and male Pacific walruses ranging in age from 2 to 45 yr. Measurements are for a flat, resting position with flippers out. Dashed lines are 95% confidence intervals

ables also exhibited good fit, residual error was higher than for models with the same variables that were not transformed. Thus, data were not transformed. Length and FFwidth were collinear (condition index = 44.5, variance proportions >0.80).

The linear model with body area was also the best fit to body mass data of 9 females ≥8 yr old (Table S2; $R^2 = 0.89$, $F_{1,11} = 75.9$, $p < 0.001$; n = 12 observations) and had an improved fit over the intercept-only model ($\chi^2 = 23.1$, df = 2, $p < 0.001$). Similar to the models with all walruses, the residual standard error on predictions from the linear model containing body area was higher (±52.4 kg) than error for the model with length and width (±49.8 kg; $R^2 = 0.90$). Similarly, models with variables that were log-transformed had larger residual error than linear models with untransformed variables. A random effect accounting for inclusion of 3 females that were measured twice at different body masses was not significant (p = 0.54). Thus, multiple regressions without random effects were used to compare candidate models. Data were normally distributed (Shapiro-Wilk = 0.87, df = 12, p = 0.07) and length and FFwidth were collinear (condition index = 46.9, variance proportions >0.65).

Area and FFwidth measures were 11.7 ± 7.8 and 20.8 ± 9.8% greater for walruses measured in a flatter, resting position versus an upright position (Fig. 8; paired t-tests: area: $t = 6.0$, df = 14, $p < 0.001$, FFwidth, $t = -8.7$, df = 15, $p < 0.001$) but there was no difference in length ($t = -1.2$, df = 14, p = 0.25). Regressions with area measured in an upright position resulted in fit (significant improvement from an intercept-only model; p < 0.001 for all models) and residual standard errors similar to models based on area measured in the flat, resting position for data sets including all walruses (±7.6%) or only adult females ≥8 yr old (±5.6%; Table S3).

3.4. Identifying sex, age, and reproductive classes for monitoring from aerial imagery

Wild female walruses reached 90% of maximum mean body length (based on zoological length measurements of harvested walruses) by 7.5 yr of age (von Bertalanffy growth curve: $y = 296.8\{1 - \exp[-0.22 (x + 2.93)]\}$, $R^2 = 0.83$, $F_{2,412} = 983.5$, $p < 0.0001$; Fig. S4). Body mass for females sampled between August and October reached 90% of maximum mean body mass by age 11.1 yr ($y = 716.4\{1 - \exp[-0.24 (x + 2.86)]\}^3$, $R^2 = 0.57$, $F_{2,1382} = 929.5$, $p < 0.0001$; Fig. S4).

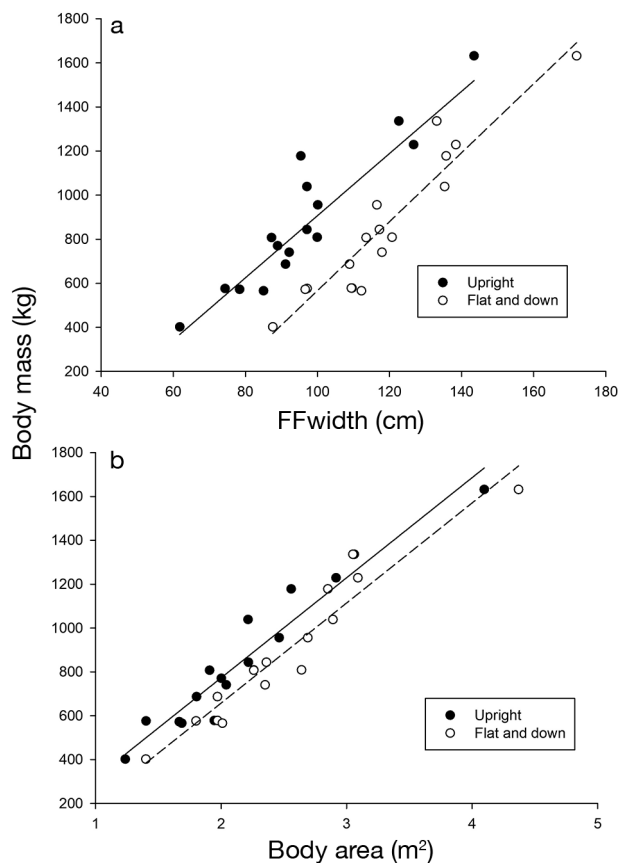Wild male walruses reached 90% of maximum mean body length (based on zoological length measure-

Fig. 8. Relationships between body mass and (a) straight-line linear width behind the front flippers (FFwidth) and (b) body area for walruses positioned upright with the head up versus walruses lying down flat

ments) by 12.6 yr of age (von Bertalanffy growth curve: $y = 354.0\{1 - \exp[-0.14(x + 3.87)]\}$, $R^2 = 0.81$, $F_{2,986} = 2095.8$, p < 0.0001; Fig. S5). Body mass for males reached 90% of maximum mean body mass by age 21.7 yr ($y = 1339.2\{1 - \exp[-0.13(x + 4.06)]\}^3$, $R^2 = 0.75$, $F_{2,1060} = 1573.0$, p < 0.0001; Fig. S5).

Seven male walruses (ages 5–40 yr) had a mean (±SD) snout width (32.1 ± 1.6 cm) measured from imagery that was 5.6 ± 0.8 (SE) cm greater than that of 10 females (ages 2–45 yr; 26.5 ± 1.6 cm; $F_{1,16} = 48.0$, p < 0.001). Data were normally distributed (Shapiro-Wilk p > 0.4) and had homogeneous variances (Levene statistic = 0.07, p = 0.80). We found complete separation in snout width between males ≥5 yr (range: 29.4–34.3 cm) and females (23.3–28.9 cm), precluding a binary logistic regression.

Using the age at which female walruses reached 90% of their maximum structural size as a separation point for using body length to classify female age, females age ≥8 yr old (n = 8, mean length = 268.7 ± 22.0) were 39.3 ± 13.9 cm longer than females that

were <8 yr of age (n = 3; $F_{1,10} = 8.0$, p = 0.23). Data were normally distributed (Shapiro-Wilk p = 0.45) and had homogeneous variances (Levene statistic = 1.99, p = 0.19). Length correctly classified 91% of females as being <8 or ≥8 yr old in a binary logistic regression ($y = 0.23\text{length} - 55.80$, Hosmer-Lemeshow goodness of fit $\chi^2 = 3.6$, df = 8, p = 0.89).

3.5. Sample sizes at haulouts

We identified an average of 216 ± 77 walruses per survey that were in 1 of the 2 positions used in our study (resting and flat or upright and moving) to estimate body mass from haulout imagery surveys collected in 2018 and 2019 (Table S4).

4. DISCUSSION

The size achieved by Pacific walruses born during the 1970s and 1980s exhibited a distinct increase and subsequent decline during a period when the population was thought to have increased, reached habitat carrying capacity, and subsequently declined. The timing of a decline in body length was later for females than males, which may reflect that males acquire body length over nearly twice as many years as females such that growth may be affected by reduced resource availability over a longer period following birth for males than females. Using birth year to examine patterns in body length identifies the earliest that resource availability may have begun to affect growth. However, reduced resource availability following birth is also likely to affect growth patterns (Pettorelli et al. 2002, Zedrosser et al. 2006), particularly during the period of lactation which lasts at least through the first year and potentially into the second year for walruses (Fay 1982). Thus, the exact timing of changes in growth are difficult to identify. However, patterns in body mass which largely reflect recent resource availability are suggestive that reduced resource availability occurred by the 1980s, consistent with declines in body length. Female walruses weighed 108 kg less in 1983 than in 1978, consistent with observation s of a sharp decline in reproduction and calf survival over this period (Fay et al. 1989) and a >100 kg decline in the body mass of adult males (this study). Although only 3 to 4 years of data on body mass were available during this period, body mass of males and females were lower in the early 1980s compared to the 1970s and 1990s. That both body length and body mass exhibit

patterns consistent with estimated demographic patterns is suggestive that the effects of food limitation on population dynamics can be detected via morphometric measures. Thus, morphometrics may be a useful additional, and relatively convenient and inexpensive, tool for tracking the status of the Pacific walrus population.

Using photogrammetric-based measures of Pacific walruses from images at resolutions that may be obtained from survey drones flown high to minimize disturbance, body mass of Pacific walruses was estimated with 5.6−6.7% error (i.e. mean difference between estimated and observed), similar to photogrammetry-based approaches developed for monitoring other marine mammals (Meise et al. 2014, Hodgson et al. 2020) including those that used 3-dimensional measures (Waite et al. 2007, Beltran et al. 2018). Error in measurement of scale markers supports that the resolution of the images provided accuracy of measurement ±1.1 cm at the substrate level where measurements occurred. At walrus haulouts, having a known size scale object within the image frame will not be possible. Thus, it is imperative that measurement accuracy be evaluated for any drone imaging system to validate that it can achieve measurement accuracy less than or equal to that achieved for the walrus aerial measurements in our study (±1.1 cm on the ~1 m scale markers).

Although the top models for estimating body mass of adult females and all sex and age classes included body area, the error associated with estimating body mass was higher than estimates from the model including length and FFwidth (Tables S1 & S2). AIC model optimization favors parsimonious models. Thus, we expect lower (more favorable) AIC scores for the single-parameter body area model than for the 2-parameter model with FFwidth and length. However, the lower residual standard error on predictions obtained from the 2-parameter model with FFwidth and length favor the use of that model. In the more upright, head-raised position, use of body area resulted in the lowest error for estimating body mass, likely because this posture changes both the FFwidth and body length. However, models with body area and with length and FFwidth had relatively similar error, particularly for adult females which differed in estimation error of only ±2.3 kg in the resting position. That the 2 models had similar error provides potentially multiple approaches for estimating body condition including (1) estimating body mass from FFwidth and length which is closely correlated with total blubber body mass in walruses (Noren et al. 2015) and (2) estimating body mass via body area and

standardizing for body length which was most closely correlated with percent blubber in adult female walruses (Noren et al. 2015). Measuring and tracking changes in both metrics for reproductive females may provide the most robust approach for detecting potential changes in body condition. Further, because FFwidth and length can be collected by Alaska Native subsistence hunters, use of these linear metrics to estimate body mass may enable additional body condition data to be collected during the spring when the bulk of the Alaska Native harvest occurs.

Although the walruses in human care in our study were positioned to allow linear measures, some minor variation in body position occurred including walruses that had flippers tucked, noses tucked (those without tusks), or head or tails with slight curvature. This contributed to the error in our measurements. However, this variation is similar to positional variation of walruses at haulouts such that our results with walruses in human care incorporated minor positional error likely encountered when measuring walruses in the wild. We also documented that body mass estimates from photogrammetry were affected by more significant variations in body position (upright moving versus flat and resting), which is consistent with previous applications for marine mammals (Waite et al. 2007, Meise et al. 2014). Thus, applying body mass estimation equations specific for each position may prove to be most useful for monitoring Pacific walrus body condition at haulouts. Estimation of body mass for walruses in both positions could be combined if similarity in trends and annual means are confirmed. That measurements made in both positions were similarly related to body mass is suggestive that there is some consistency in the degree to which walruses push up on their front flippers while moving. Nonetheless, further investigation into the degree to which walruses at haulouts can be accurately classified as moving and upright versus resting and potential individual measurement variation in the upright, moving posture could help improve the accuracy of body mass estimation.

Consistent with frontal-based differences in male and female snout width (Fay & Kelly 1989), our data supported a complete separation in aerial imagery-based measurement of snout widths of males ≥5 yr of age and females of all ages. That this separation was detected from imagery-based measurements at resolutions typical of drone imagery suggests that females can be accurately differentiated from males that are ≥5 yr of age even at imagery resolutions ±1 cm. Our finding that females reach 90% of their adult body length by approximately 8 yr of age is

similar to findings for wild walruses measured by Fay (1982) and growth patterns observed in walruses in human care (9.8 yr for the lower end of the 95% confidence interval of adult length applying a Gompertz growth curve). Because most growth in length is achieved by females by the age of 8 yr, which corresponds with the age at which all females have ovulated and in which conception and gestation are highest (Fay 1982, Garlich-Miller et al. 2006, Robeck et al. 2022), our ability to accurately categorize 91% of females as ≥ or <8 yr old based on body length indicates that this is a useful measure for identifying reproductive-age females (Monson et al. 2013, this study). Male and female walruses do not differ in size before the age of 3 (Noren et al. 2015, Katsumata et al. 2020) and therefore determination of their sex would not be required for monitoring trends in growth and body condition of these age classes. Their growth could be monitored based on length alone since increases in structural size are concurrent to increases in body mass (Noren et al. 2016) and 1-dimensional measures, avoiding compounding of error (Bierlich et al. 2021). Within our data set, we had two 3 year olds, a male and female, but no younger (dependent) walruses. Thus, estimating body mass of dependent walruses would involve extrapolation of our models outside of the data, thereby potentially increasing error — another factor supporting that body length of dependent young may be the least biased metric to monitor their size.

Assessment of haulout imagery collected in 2018 and 2019 suggest that >200 Pacific walruses may be positioned for measurement from a single survey image. Nearly all of these individuals occurred at the edge of the haulout and primarily on the landward side (Fig. 4). This included an average of 25 calves and 19 females accompanied by calves. These estimates are minimums because the surveys were not designed to support walrus measurement and often lacked clarity to determine whether walruses were adequately positioned for measurement. The majority of walruses identified are likely reproductive-age females based on the known demography of the coastal haulout (<1% males, >60% adult females, Monson et al. 2013). Because the haulout involve tens of thousands of walruses, the small proportion of animals suitably positioned for measurement in a single image minimizes the risk of resampling the same individuals during subsequent surveys. Jay et al. (2017) found that walruses using this large coastal haulout rested out of water <9% of the time, consistent with rapid fluctuations in haulout size (Fischbach & Douglas 2021). Thus, sample sizes of measured walruses can be increased via repeated imagery taken throughout the duration of the haulout season, generating sample sizes of approximately 3500 if sampled every other day or 7000 if sampled daily. Although this represents a small proportion of the total population (3500–7000 of >100 000 animals), frequent movement of individuals into and out of the haulout for foraging are suggestive that walruses on the herd edge are not a biased sample (i.e. that body condition and size are not related to position at the haulout), but rather individuals that are coming into and out of the herd. However, Monson et al. (2013) did identify that females with calves may be more likely to occur on the herd edge. Further investigation of patterns in body condition relative to location in the herd would be informative to the potential for demographic sampling biases. Additionally, data on individual residence times at the haulout from tagging data, an analysis that is currently underway, would be useful to inform a sampling frequency that would minimize repeated sampling of individuals.

Marine mammals are some of the most challenging species to study in the wild due to limitations of our ability to observe their behavior and to physically assess their health (Booth et al. 2020). The pace at which ecological change is occurring in the Arctic has created a particular demand for new tools to monitor Arctic marine species (Kovacs et al. 2011, Serreze et al. 2016, Huntington et al. 2020). Combined, our results provide an approach for monitoring the body condition of reproductive-aged females and size of calves of Pacific walruses, classes that are most vulnerable to environmental change and most reflective of population recruitment. The reliance of Pacific walruses on a highly productive Arctic benthos (Sheffield & Grebmeier 2009) make them a bellwether for environmental changes that may have broader ecosystem effects and further emphasize the value of new tools for monitoring Arctic marine mammals.

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