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Validation of the photogrammetric method to assess body condition of an odontocete, the short-finned pilot whale *Globicephala macrorhynchus*

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ABSTRACT: Validated metrics to monitor body condition of free-ranging animals are critical to track population stability. We tested repeatability and reliability of body width and body length measurements taken from overhead photographs and validated the assumptions upon which the photogrammetric method to monitor cetacean body condition are based. Short-finned pilot whales *Globicephala macrorhynchus* served as models. Variability was low for multiple measurements taken from 1 photograph and across photographs of the same animal; standard deviations represented 1.2 ± 1.2% and 2.5 ± 1.3% of mean estimates, respectively. To account for body length variations across whales, we calculated mass, width, and blubber indexes as the residual values of these variables regressed against length. Across the sites examined (anterior pectoral fin, anterior dorsal fin, and posterior dorsal fin), only photogrammetric body width at the posterior dorsal fin site showed consistent significant positive relationships with measured condition indexes (i.e. width and blubber index slope = 0.10, $p = 0.005$; width and mass index slope = 18.1, $p < 0.01$). Moreover, only the body width to body length ratio at this site predicted mass index (slope = 3105, $p = 0.05$). Thus, changes in photogrammetrically measured body width posterior of the dorsal fin at approximately 47% of total body length from the rostrum are related to changes in underlying blubber thickness and body mass. The width:length ratio at this site can be used to monitor condition. Additional studies are warranted to determine if body width at this site reliably predicts condition across odontocete species with varying body morphologies.

KEY WORDS: Photogrammetry · Body condition · Blubber · Pilot whale · Odontocete · Disturbance

1. INTRODUCTION

Body condition, a metric used to estimate relative energetic reserves, has been correlated with survival and reproductive success of both terrestrial (Young 1976, Schulte-Hostedde et al. 2001) and marine (i.e. Lockyer 1986, Pitcher et al. 1998, Hall et al. 2001) mammals. It is often used to assess and monitor the overall health of animal populations (i.e. Beck et al. 1993, Gerhart et al. 1996, Williams et al. 2013). The energetic reserves in cetaceans, pinnipeds, and polar bears are primarily stored in a unique tissue called blubber, a layer between the epidermis and the underlying muscles (Parry 1949). Blubber is composed of numerous adipocytes where energetic reserves can be mobilized and play an important role in metabolism (Chen & Farese 2002). Thus, blubber thickness in marine mammals is considered indicative of body condition, or the general measure of an animal's energy reserves (i.e. Read 1990, Ryg et al. 1990a,b, Renouf et al. 1993).

For many free-ranging marine mammals, large body sizes and fully aquatic life histories make it difficult to use conventional methods to assess body

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condition. Some traditional methods to measure body condition, outside of simply weighing the animal, include bioelectrical impedance (Gales & Renouf 1994, Arnould 1995, Bowen et al. 1999), isotope dilution (Costa 1987, Reilly & Fedak 1990, Noren et al. 2008), and ultrasonic techniques (Slip et al. 1992, Mellish et al. 2004, Noren & Wells 2009). With the exception of ultrasonic methods recently developed to measure the blubber thickness of free-ranging baleen whales (Moore et al. 2001, Miller et al. 2011), all of the aforementioned methods require capturing, restraining, and often sedating the animal. Consequently, there is value in further identifying and validating non-invasive methods to measure the body condition of free-ranging marine mammals.

Recently, photogrammetry has been used to estimate the body condition of marine mammals. For cetaceans (dolphins and whales), this method has primarily been used with large-bodied mysticete (baleen whales) species. Variations in photogrammetrically measured body widths have been detected in blue whales *Balaenoptera musculus* (Durban et al. 2016), humpback whales *Megaptera novaeangliae* (Christiansen et al. 2016), right whales *Eubalaena glacialis* and *E. australis* (C. Miller et al. 2012, Christiansen et al. 2018), and gray whales *Eschrichtius robustu*s (Perryman & Lynn 2002), but these studies were cross-sectional. These studies did not demonstrate that changes in body width within an individual are due to changes in the underlying blubber thickness at that body location in accordance with overall body condition (body mass). To assess body condition, it is preferable to measure body width at sites where blubber is most variable in accordance with metabolic needs (Lockyer et al. 1985), as blubber thickness should change as adipose cells shrink and swell during periods of fasting and fattening (Young 1976, Pond 1998). Shrinking and swelling of adipose cells, rather than a change in the numbers of adipocyte cells, has been well studied in terrestrial mammals (see Young 1976 and Pond 1998 for reviews) and other aquatic animals adapted for routine fasting, such as emperor penguins *Aptenodytes forsteri* (Groscolas 1990) and polar bears *Ursus maritimus* (Ramsay et al. 1992). In some regions of the body, however, blubber does not act as an energy reserve; it serves to streamline the body, insulate the core, and adjust buoyancy (Ryg et al. 1988), such that these regions of blubber will not readily respond to changes in energy balance.

Fewer studies have attempted to track the body condition of free-ranging odontocetes (toothed whales and dolphins) using photogrammetry. Unlike mysticetes, odontocetes do not rely on large endogenous reserves to support reproduction and migration. As a result, odontocetes will have less profound changes in body morphology during life history events. Moreover, to obtain accurate measurements when using photogrammetric methods, the contour of the animal's body needs to be clearly visible; however, waves, water spray, and turbidity can distort body contours in a photograph (Christiansen et al. 2016). For smaller-bodied animals, the noise-to-signal ratio will likely be higher, which could limit the application of photogrammetric methods to identify subtle changes in odontocete body width. Although some attempts have been made to use photogrammetric methods with free-ranging beluga whales *Delphinapterus leucas* (Suydam 2009) and bottlenose dolphins *Tursiops truncatus* (Gryzbek 2013), without validation studies or knowledge of the animals' body masses and blubber thicknesses it is unclear what range of body conditions the measured body width to body length ratios represented.

Validating the assumptions of the photogrammetric method and testing the application of this method with smaller-bodied odontocetes is important, as anthropogenic disturbances in the marine environment (i.e. noise) are poised to impact the status of numerous species, particularly when disturbance reduces feeding rates (Miller et al. 2009). Indeed, long-finned pilot whales *Globicephala melas* change diving (Sivle et al. 2012) and vocal behavior in response to sonar exposure (Rendell & Gordon 1999, Alves et al. 2014) and show avoidance and reduce foraging (Antunes et al. 2014). Alterations in behavior and foraging in response to sonar have also been observed in killer *Orcinus orca* (P. Miller et al. 2012, 2014), beaked (Tyack et al. 2011, DeRuiter et al. 2013), blue (Goldbogen et al. 2013), and sperm *Physeter macrocephalus* (P. Miller et al. 2012) whales. Over the long term, repeated changes in foraging behavior could lead to a decline in body condition of individuals, which can have profound population consequences (i.e. New et al. 2014, McHuron et al. 2017, Pirotta et al. 2018).

The aims of this study were to (1) ground-truth the assumption that body width measurements taken from overhead photographs vary with changes in the thickness of the underlying blubber layer in accordance with changes in overall body condition (body mass), (2) assess the reliability and repeatability of using this method on smaller-bodied odontocetes that are not undergoing fasting periods, and (3) determine which site along the body provides the most sensitive measure for changes in condition in an odontocete. To accomplish these goals, we conducted a controlled longitudinal study on short-finned pilot whales

G. macrorhynchus (n = 6) held in aquaria for nearly 2 yr. We examined variations within and across individuals in body width measured from overhead photographs in relation to variations in the underlying blubber thickness and body girth measured at that site, as well as changes in overall body mass.

2. MATERIALS AND METHODS

2.1. Animals

Sexually immature and mature, healthy short-finned pilot whales in managed care at SeaWorld San Diego (California, USA) (n = 1 male and 1 female) and Orlando (Florida, USA) (n = 1 male and 3 females) were studied at 5 different intervals for nearly 2 yr (see Table 2). Throughout the longitudinal study, water temperature varied, ranging from 15.51 to 25.39°C (average ± SD = 20.29 ± 2.85°C) and 13.00 to 25.20°C (average ± SD = 19.2 ± 3.90°C) at SeaWorld San Diego and Orlando, respectively, and there were marked variations in blubber thickness and body mass within each whale. The approach of doing longitudinal studies of marine mammals in managed care to validate metrics to monitor body conditions of free-ranging animals was recently used with another difficult-to-study marine mammal, the Pacific walrus *Odobenus rosmarus divergens* (Noren et al. 2015). Standard operant training protocols were used to desensitize the whales to the protocols and scientific equipment (scale, tape measure, and ultrasound probe).

2.2. Body mass, morphology, and blubber thickness measurements

Whales were typically weighed weekly by beaching on a platform scale. All tape measure (straight line body length on the ventral surface, a series of girth measurements, and the straight-line distance from the beak to each girth location) and all blubber thickness (mid-line dorsal, mid-line lateral, and mid-line ventral at each girth site) measurements were taken while the whales remained in the water because beaching can cause deformation of the blubber layer. Girth measurements were taken at 5 sites along the body, including anterior pectoral fin, anterior dorsal fin, posterior dorsal fin, mid-genital slit, and midway between the genital slit and fluke insertion, termed 'mid-peduncle.' These sites were adapted from Doidge (1990) and Noren et al. (2015). Similar to methods used with dolphins, girth measurements were taken by wrapping a tape measure around the animal (S. Noren unpubl. data). Blubber thickness measurements were taken using a portable ultrasound (M-Turbo, SonoSite; Fig. 1) as in Noren et

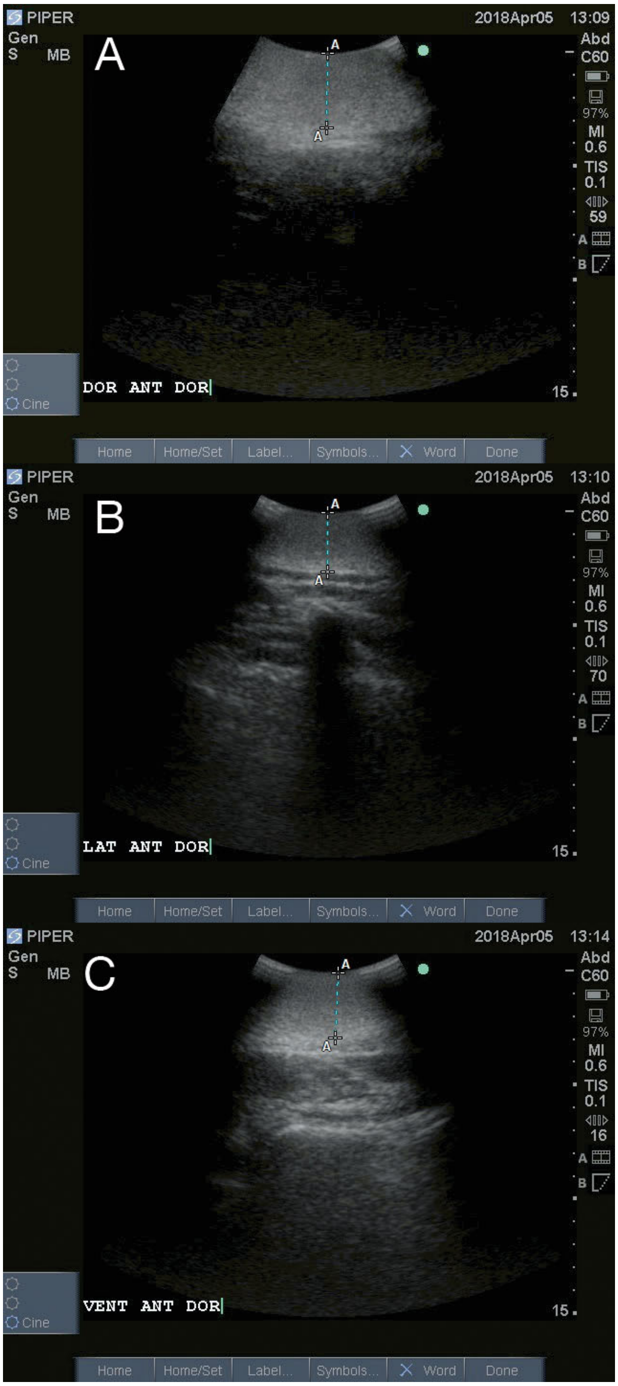

Fig. 1. Three ultrasound images taken along the anterior dorsal fin girth location, (A) mid-dorsal (DOR ANT DOR), (B) mid-lateral (LAT ANT DOR) and (C) mid-ventral (VENT ANT DOR), for an adult female pilot whale during one of the sample intervals. Blue dashed line represents blubber thickness

al. (2015). Dorsal and lateral blubber thicknesses were measured while the whales were in ventral recumbency in the water, and ventral blubber thicknesses were measured while the whales were in dorsal recumbency in the water. Measurements of blubber thickness using ultrasound have been validated in dolphins by comparing to blubber biopsies (S. Noren unpubl. data).

2.3. Photogrammetry

Overhead photographs were taken with an EOS-1DX Mark II Canon camera with an EF50mm f/1.8 STM lens and an WFT-E8 wireless file transmitter attachment that enabled remote operation via a laptop (HP Notebook with a 6th Gen Intel Core i5-6200U Processor, 8GB DDR3L SDRAM, 1TB HDD, Windows 10 operating system). A full-sensor camera was chosen for the purpose of this validation study to maximize megapixels, and hence the quality of the photographs. Specifications for this camera and cameras that have been used in recent field photogrammetry studies of cetaceans are provided in Table 1; technology will continue to improve so that the quality of photographs obtained from lightweight cameras will continue to improve. The camera was housed in an Outex waterproof rubber sleeve and fixed to an overhead beam at 9.4 m over the water surface at SeaWorld San Diego. For SeaWorld Orlando, the camera was fixed to either an overhead beam or an articulating boom lift such that the camera was 6.1–12 m off the water surface. A mini level was attached to a flat surface on the external housing of the camera to ensure that the camera lens was parallel to the plane of the water surface after it was fixed. Distance from the camera to the water surface was estimated by dropping a rope from the fixture point to a person floating below the camera; the length of rope was then measured.

Each whale swam underneath the camera (in frame) back and forth between 2 trainers (a behavior called 'A to B') during 10–15 min sessions. The whales swam straight and upright (no listing) with their dorsal side up. Wake and water splash were minimized by having the whales swim slowly. Refraction in the photographs was minimized by having the whales swim at the surface. With the exception of the peduncle region, this approach provided for crisp edges of the whales' bodies in the photographs to facilitate subsequent body width and body length measurements (Fig. 2). *A priori*, to obtain accurate measurements when using photogrammetric methods, the contour of the animal's body needs to be clearly visible (Christiansen et al. 2016). Thus photogrammetric body width measurements were only taken at the anterior pectoral fin, anterior dorsal fin, and posterior dorsal fin sites because the body contours at the mid-genital slit and mid-peduncle sites were occluded by wake and water splash and were often submerged below the waterline (Fig. 2).

A total of 2740 photographs were captured during this study. From these, the 5 best photographs were chosen for each whale within each data collection interval. All of the photographs chosen had the whales' entire bodies in frame, their bodies appeared to be straight and streamlined with no listing, and the peduncle appeared to be neutral (not in an upstroke or downstroke). There was also minimal wake, water splash, refraction, or glare from the sun on the water so that the contours of the whales' bodies were comparatively crisp compared to other photographs that were taken. Image J software was used to measure total body length and body widths at the anterior pectoral fin, anterior dorsal fin, and posterior dorsal fin sites, which on average were located at 17, 28, and 47% of total body length from the rostrum, respectively.

Briefly, the analysis process within Image J began by using the magnifying tool to magnify the image 2 times. The scale for the measurements was set from the known lengths (105–248 cm) of a painted line on the pool edge or a target pole on the pool deck (secured with SCUBA diving weights) that was adjacent and parallel to the whale and within frame. The software transposed pixels into units of measure according to the scale, and then body width and length were measured. Each photograph was analyzed 3 times to test repeatability and reliability within a photograph.

Table 1. Camera specifications that affect picture quality for the camera used in this study compared to cameras used in recent photogrammetric studies of cetaceans in the field with hexicopters and drones

Camera	Sensor size (mm)	Effective megapixels	Studies
Canon 1DX Mark II	36 × 24	20.2	This study
Olympus E-PM2	17.3 × 13	16	Durban et al. (2015, 2016)
Canon PowerShot D30	6.17 × 4.55	12	Christiansen et al. (2016)
GoPro Hero 7	6.17 × 4.55	12	None available

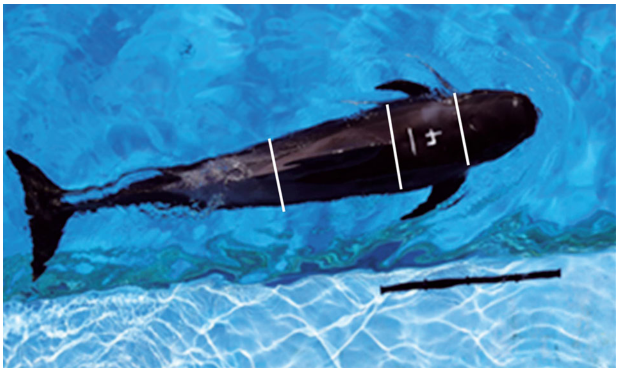

Fig. 2. Photograph of pilot whale no. 4 taken from overhead. Colored zinc oxide was used to mark the whales with their identifying number and to draw a line near the anterior insertion of their dorsal fin. Body width measurements (heavy white lines) were only possible at 3 of our 5 morphological sites (anterior pectoral fin insertion, anterior dorsal fin insertion, and posterior dorsal fin insertion) because the body contours of the peduncle were occluded by waves. Body length was also measured from the photographs. The black line in the photograph is a painted line on the pool edge that provided the scale for the photographic measurements

Repeatability and reliability were further tested by comparing measurements taken from 5 different photographs for each whale during each sample interval.

2.4. Measurement error

To understand uncertainty in the photogrammetric technique, we quantified and compared variability in photographic measurements of length and widths from repeated samples of the same whale on the same day. Reliability and repeatability when using photogrammetry to estimate body width and body length were examined by exploring the variation in these measurements done in triplicate from each photograph. We used 2-way ANOVA with an interaction term to examine potential differences in the log of standard deviations in photographic measurements by individual and location on the body. After determining the significance of individual and body location, we examined if the magnitude of the measurement played a role in photographic measurement uncertainty. To determine repeatability between photographs, we also examined the variation in body width and body length measurements taken from 5 different photographs of the same animal during the same sample interval. Using 2-way ANOVA, we examined if the variability across photographs differs by individual, location on the body, and magnitude of the measurement.

2.5. Total body length estimation

To isolate and determine the best photographic width for estimating body condition, we needed to first establish a body length estimate for each animal at each sample interval since measurements across whales needed to be standardized by body length to account for size variations across the whales in this study. Preliminary analysis determined a potential error in some of the tape-measured body lengths. For the 3 whales known to have achieved mature body length, variation in total body length using a tape measure was 4–15 cm across sample intervals. For the 3 whales still growing, variation in tape-measure body length was 12–55 cm across sample intervals and was not consistently increasing.

Using photographic total body lengths also presented a challenge, because total body length from photographs was 15.3 ± 16.9 cm shorter than tape-measured length, such that, on average, tape-measured lengths were 3.4 ± 4.1% longer than photographic lengths. This result may be associated with the peduncle not being perfectly aligned with the body when the photograph was taken, i.e. the animal may have been slightly in an upstroke or downstroke which would make the animal appear shorter. However, total body lengths from photographs were consistently increasing for the 3 immature whales.

We assumed that the 2 adult whales and the older juvenile whale were not growing in length, and their average tape-measured body lengths across sample intervals was used as their 'adjusted body length.' Any variability was considered a relatively small measurement error with standard deviations of 2, 2, and 8 cm, representing <0.6% of the mean for the adults and 1.8% of the mean for the older juvenile. We estimated linear regression relationships for age versus body length from the 5 photographs across sample intervals for each growing whale to address growth that was occluded by potential measurement errors when using the tape measure. A linear estimate sufficed because the study was short compared to the long-term non-linear growth of an animal over its lifetime (Fig. 3). The body lengths derived from the linear regression relationships were then adjusted to account for the difference between photographic and tape measure total body lengths. Thus, 'adjusted body lengths' for the growing whales accounted for growth seen in the photographic measurements and the negative bias in photographic total length measurements (Fig. 3). The adjusted body lengths described above were used in all subsequent analyses when standardizing any metric to length.

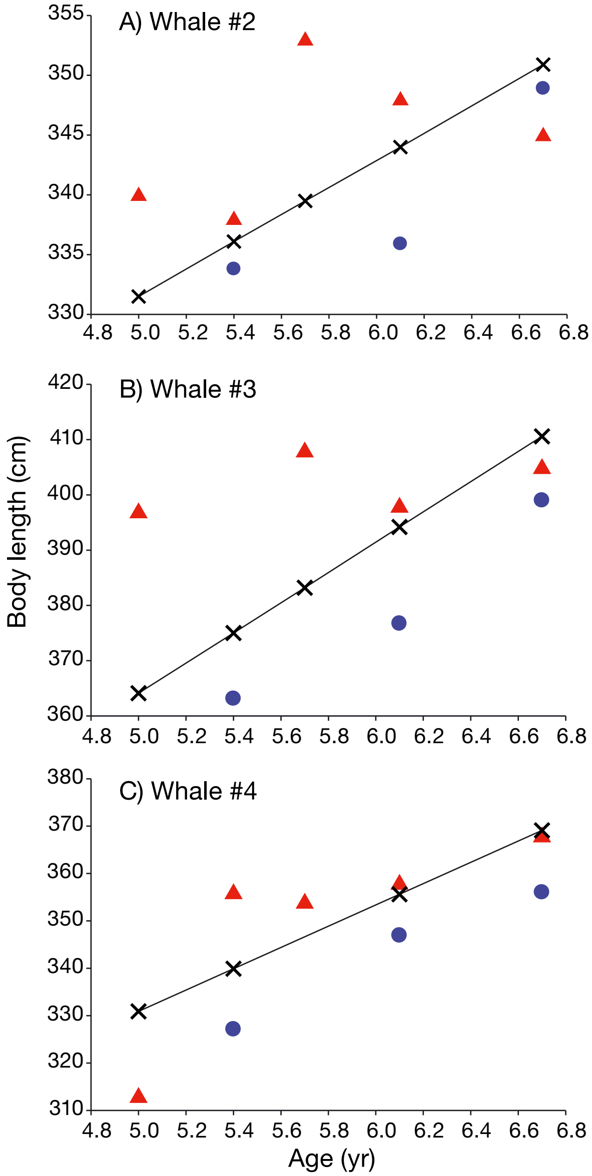

Fig. 3. (A–C) Total body length at a given age for the 3 pilot whales that were growing throughout the study. Blue circles represent the mean length measured from photographs, red triangles represent the corresponding tape-measured length, and black crosses connected with a black line represent the 'adjusted body length' based on estimates of total length from linear regressions of age versus photographic length adjusted for the negative bias in photographic measured length versus tape-measured length as described in Section 2.5

2.6. Standardizing for total body length

The 6 whales varied in body length, and 3 of the 4 juvenile whales were growing throughout the study. This variation in body length across individuals and within individuals across sample intervals impacts the magnitude of the blubber thickness, body mass, and body width measurements. Therefore, these metrics had to be standardized by body length before subsequent analyses. The average of the blubber thicknesses measured dorsally, laterally, and ventrally at each of the 3 girth measurement sites, body mass, and photographic body width measured at each of the 3 girth sites (Table 2) were standardized by the whale's body length at that sample interval. We term these length corrected measurements, blubber index, body mass index, and body width index.

Both piecewise and segmented regression suggested a change in the relationship between blubber and adjusted length at 365 cm. Therefore, the blubber index was defined as blubber thickness values standardized by the mean thickness for animals <365 cm or ≥365 cm long; each of the 3 locations was considered separately (Fig. 4A). The mass index was calculated as the residual value of mass from the linear regression analysis of mass versus length (Fig. 4B). When determining the body width index, each of the 3 locations was considered separately. The mean of the triplicate measurements from each photograph was combined across the 5 photographs analyzed per whale per sample interval to calculate a grand mean for that body width site, which served as the estimate of body width. Using Akaike's information criterion corrected for small sample size (AICc), we determined the best-fitting model, and the width index was calculated as the residuals of the asymptotic relationship:

$$\text{Body width}_l = \beta_0 + (\beta_{1l} \times \text{Length}^{-1}) \quad (1)$$

where β_0 = intercept, and β_{1l} = slope, specific to body location (l) (Fig. 4C).

A priori, based on basic geometric assumptions, the relationship between body girth and body width at the same site should be independent of animal length. Thus, when the relationship between girth and body width at each of the 3 sites was examined, these variables were not standardized for body length.

2.7. Relationship analyses

We examined how each photographic body width measurement varied with actual measurements of body condition, specifically underlying blubber thickness and girth at that same site as well as body mass. Blubber index was examined as a linear function of body width index at the matching body location; a similar analysis was done for the relationship between body width and body girth at the matching body location. Mass index was examined as a linear function of body width index for each of

Table 2. Summary of corrected body length, body mass, and tape-measured girth, photogrammetrically measured width, and the average of the blubber thicknesses measured mid-dorsal, mid-lateral, and mid-ventral at the anterior pectoral fin sites (1), anterior dorsal fin site (2), and posterior dorsal fin site (3) for each individual short-finned pilot whale (—, 0, 1, 2, 3, and 4) during each sample interval. NA denotes missed measurements

Photo ID	Date (yr-mo)	Age (yr)	Mass (kg)	Adjusted length (cm)	Girth 1 (cm)	Girth 2 (cm)	Girth 3 (cm)	Width 1 (cm)	Width 2 (cm)	Width 3 (cm)	Blubber 1 (cm)	Blubber 2 (cm)	Blubber 3 (cm)
__	16-Aug	14	894	447	210	NA	217	NA	NA	NA	3.57	2.56	3.01
__	16-Dec	14.4	864	447	NA	NA	NA	59.9	61.1	51.2	3.51	2.59	2.91
__	17-Apr	14.7	876	447	197	224	201	61.1	61.9	50.3	3.23	2.87	3.06
__	17-Aug	15.1	866	447	202	216	187	60.7	62.1	51.3	3.55	2.77	3.16
__	17-Dec	15.3	958	447	207	223	209	61.6	64.1	53.8	3.52	3.37	3.16
0	16-Aug	37.1	841	424	191	231	203	NA	NA	NA	3.33	2.55	3.11
0	16-Dec	37.4	841	424	194	230	200	58.1	65.1	51.5	3.26	2.58	2.92
0	17-Apr	37.7	891	424	196	231	212	57.5	62.3	52.2	3.36	2.76	3.29
0	17-Aug	38.1	875	424	193	232	201	57.9	65.0	52.7	3.22	2.73	3.05
0	17-Dec	38.4	883	424	195	239	209	58.6	62.9	51.9	3.39	2.83	2.64
1	16-Aug	6	620	375	171	228	197	NA	NA	NA	2.74	2.85	3.13
1	16-Dec	6.4	665	375	171	224	187	56.7	61.8	48.8	3.07	3.09	3.47
1	17-Apr	6.7	721	375	169	234	205	NA	NA	NA	2.52	2.91	3.16
1	17-Aug	7.1	NA	375	185	230	208	57.7	63.5	49.9	3.29	3.11	3.26
1	18-Apr	7.7	762	375	192	236	201	58.8	67.2	49.9	3.17	3.62	3.68
2	16-Aug	5	540	332	166	208	176	NA	NA	NA	2.67	2.49	2.73
2	16-Dec	5.4	565	336	163	214	177	53.7	58.0	44.4	2.70	2.56	2.76
2	17-Apr	5.7	621	340	169	215	186	NA	NA	NA	2.54	2.40	2.58
2	17-Aug	6.1	626	344	183	215	183	52.7	58.5	43.8	2.76	2.41	2.56
2	18-Apr	6.7	635	351	185	220	191	54.0	61.2	49.4	2.59	2.54	2.70
3	16-Aug	5	708	364	175	222	192	NA	NA	NA	2.63	2.73	2.94
3	16-Dec	5.4	730	375	175	220	181	58.8	61.2	48.6	2.63	2.79	3.07
3	17-Apr	5.7	821	383	176	229	202	NA	NA	NA	2.59	3.05	2.81
3	17-Aug	6.1	798	394	192	228	197	58.1	63.8	50.5	3.04	3.33	3.36
3	18-Apr	6.7	880	411	216	243	210	59.7	66.4	55.6	2.90	3.47	3.89
4	16-Aug	5	524	331	164	206	178	NA	NA	NA	2.69	2.49	2.27
4	16-Dec	5.4	533	340	168	194	169	53.9	57.4	43.5	2.87	2.56	2.45
4	17-Apr	6.1	NA	356	162	218	183	NA	NA	NA	2.47	2.39	2.44
4	17-Aug	6.1	608	356	185	211	186	54.6	60.6	47.2	2.75	2.59	2.41
4	18-Apr	6.7	635	369	183	213	195	57.5	62.7	47.8	2.79	2.90	2.91

the 3 sites. Lastly, we quantified the relationship between body width divided by body length (body width:length ratio) and mass index for each site. The site where the body width:length ratio best predicts the mass index can be used as a proxy for condition for free-ranging odontocetes. For all of these analyses, the 3 body locations were examined separately, and different models were compared using AIC to determine if model fit improved with inclusion of differences in slope and/or intercept by individual. For all analyses, we used library 'lmerTest' in R (Kuznetsova et al. 2017) to determine AICc and p-values for random effects models and for comparing AICc values using ANOVA. The Shapiro-Wilk test was used to determine normality of response variables. Only measurement error standard deviations were log transformed to ensure normality. Results of the Breusch-Pagan test implied homoscedasticity.

3. RESULTS

Across sample intervals but within individual whales, body mass, body girths, average blubber thicknesses, and body widths varied by 1.1–1.2, 1.0–1.2, 1.1–1.4, and 1.0–1.1 times during the course of this study, respectively (Table 2). Combining all data across all whales and sample intervals provided for greater variation. Body mass varied by 1.8 times from the lightest to heaviest whale, with the result that body girth varied by 1.3 times at each of the 3 sites, the underlying average blubber thicknesses varied by 1.5 at the anterior pectoral and anterior dorsal fin sites and by 1.7 times at the posterior dorsal fin site, and body width varied by 1.2 times at the anterior pectoral and anterior dorsal fin sites and by 1.3 at the posterior dorsal fin site. Thus, this longitudinal and cross-sectional approach captured variations in body mass within and across individuals that provided for

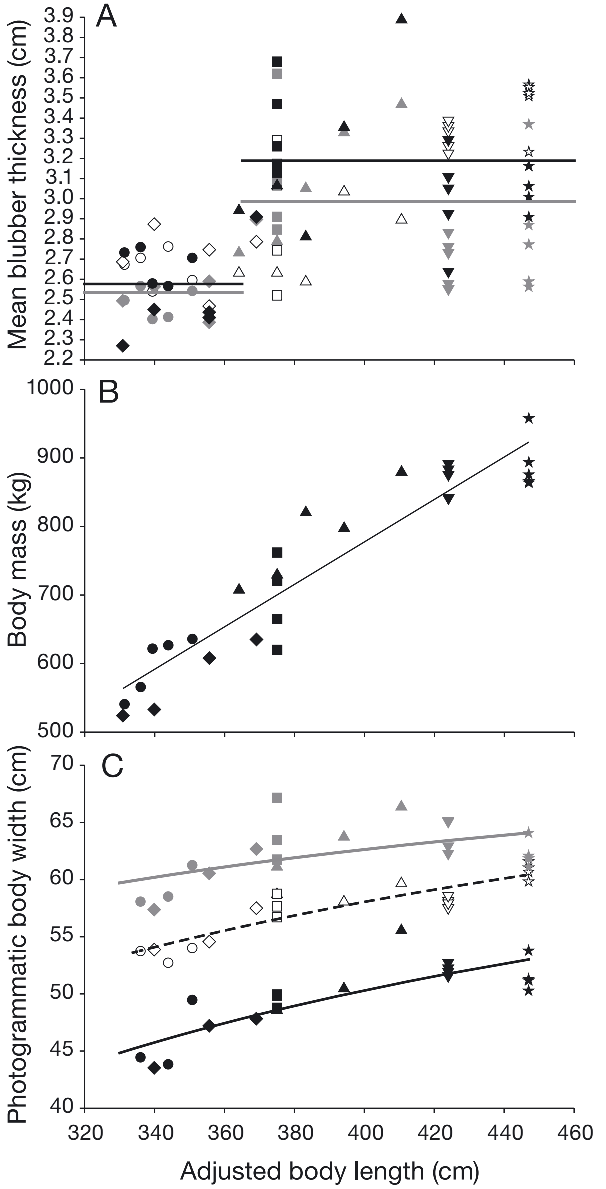

Fig. 4. Body length standardization of (A) blubber thickness, (B) body mass, and (C) body width measured from photographs of pilot whales. Blubber indexes (A) were calculated as the difference between the measured blubber thickness and the mean estimate of blubber thickness, which varied by body location and was different for animals <365 cm and ≥365 cm long. Mass indexes (B) were the residuals of each mass data point from the linear relationship between mass and length, where Mass = 3.09 × Length − 475.78 ($r^2 = 0.86$, $p < 0.01$). Body width indexes (C), were calculated as the residuals of the asymptotic relationship given in Eq. (1), such that Pectoral Fin Width = 77.7 − 6019.5 $(\text{Length})^{-1}$, Anterior Dorsal Fin Width = 77.7 − 7887.8 $(\text{Length})^{-1}$, and Posterior Dorsal Fin Width = 77.7 − 10925.3 $(\text{Length})^{-1}$. Each individual whale is represented by a unique symbol. The data and relationships for the anterior pectoral, anterior dorsal, and posterior dorsal fin sites are denoted by white symbols and dashed black line, dark gray symbols and dark gray line, and black symbols and black line, respectively

variations in body girth and underlying blubber thickness, as well as variation in body width measured from overhead photographs. This variation enabled us to achieve the goal of validating the assumptions of the photogrammetric technique to monitor cetacean body condition and testing the reliability of using this technique on smaller-bodied cetaceans.

3.1. Measurement error

Within-photo measurement variability (natural log of standard deviation from 3 measures of the same photograph) was significantly different by individual, body location, and the interaction of individual and body location ($R^2 = 0.144$, $p < 0.01$). However, no individual had consistently lower or higher variability within photographs by body location. Likewise, no body location had consistently lower or higher variability within photographs by individual. Standard deviation of measurements within a photo was lowest at the anterior dorsal fin measurement site (0.68 ± 0.56 cm), followed by total body length (0.80 ± 0.54 cm) and anterior pectoral fin measurement site (0.90 ± 0.51 cm), and highest for the posterior dorsal fin measurement site (0.95 ± 0.75 cm). Compared to overall mean measurements (Table 2), variability was small for multiple measurements taken from 1 photograph, with standard deviations representing 1.2 ± 1.2% of mean estimates.

While some individuals had statistically significant changes in within-photo variability as a function of the average measurement, the direction of that change was not consistent across individuals or body location. Removing individual and combining width measurements, variability declined as average width increased (coeff = −0.015, p = 0.027). Conversely, length measurement uncertainty increased as average length increased (coeff = 0.005, p = 0.003). However, R^2 values were low in both cases (0.016 and 0.086, respectively), suggesting that these results are not biologically meaningful.

When exploring between-photo variability for the same individual within each sample interval, mean values of each body width and body length for each photograph were compared. Variability across photographs of the same individual within a sample interval was also low, with standard deviations representing 2.5 ± 1.3% of mean estimates. Standard deviations were lowest at the anterior dorsal fin measurement site (1.3 ± 0.5 cm), followed by the anterior pectoral fin measurement site (1.5 ± 0.7 cm) and the posterior dorsal fin measurement site (1.7 ± 0.6 cm), and highest for total body length (7.4 ± 4.6 cm); between-photo variability was not different by individual or body location. Variability did not significantly change with an increase in average measurement, for either body width or body length.

3.2. Relationship analyses

When exploring the relationship between photographic body width index and blubber thickness index, the strongest positive relationship was at the posterior dorsal fin site ($p < 0.01$). The blubber index and width index at the anterior dorsal fin site were also positively correlated; however, the p-value was just over 0.10. Meanwhile, body width index and blubber thickness index at the anterior pectoral fin site were negatively correlated (Fig. 5). Model fit for the posterior dorsal fin site was not improved with individual estimates for slope or intercept. Conversely, the model estimate for the anterior pectoral fin site was improved by individual estimates for intercept, and the model estimate for the anterior dorsal fin site was improved by individual estimates for slope and intercept (Table 3). The positive and significant relationship for photo body width index with blubber index at the posterior dorsal fin site, where individual was not important, suggests that measurements of body width at this location reliably track changes in blubber thickness that are not individual specific. Therefore, body width measurements at the posterior dorsal fin site may be a good indicator of condition for the population.

Tape-measured body girth was significantly and positively correlated with photographic body width at all 3 body locations (Fig. 6). Model fit for the relationship between photogrammetrically measured body width and tape-measured body girth at the anterior pectoral and posterior dorsal fin sites were not improved with individual estimates for slope or intercept, while the model estimate for the anterior dorsal fin site was improved by individual estimates for intercept (Table 3).

Mass index was positively correlated with width index at all 3 sites, but this relationship was only significant for the anterior and posterior dorsal fin sites using a $p < 0.05$ criterion (Fig. 7). Model fit was not improved with individual estimates at the anterior dorsal fin site, but it was improved by individual estimates of slope for the posterior dorsal fin site and individual estimates for intercept for the anterior pectoral site (Table 3).

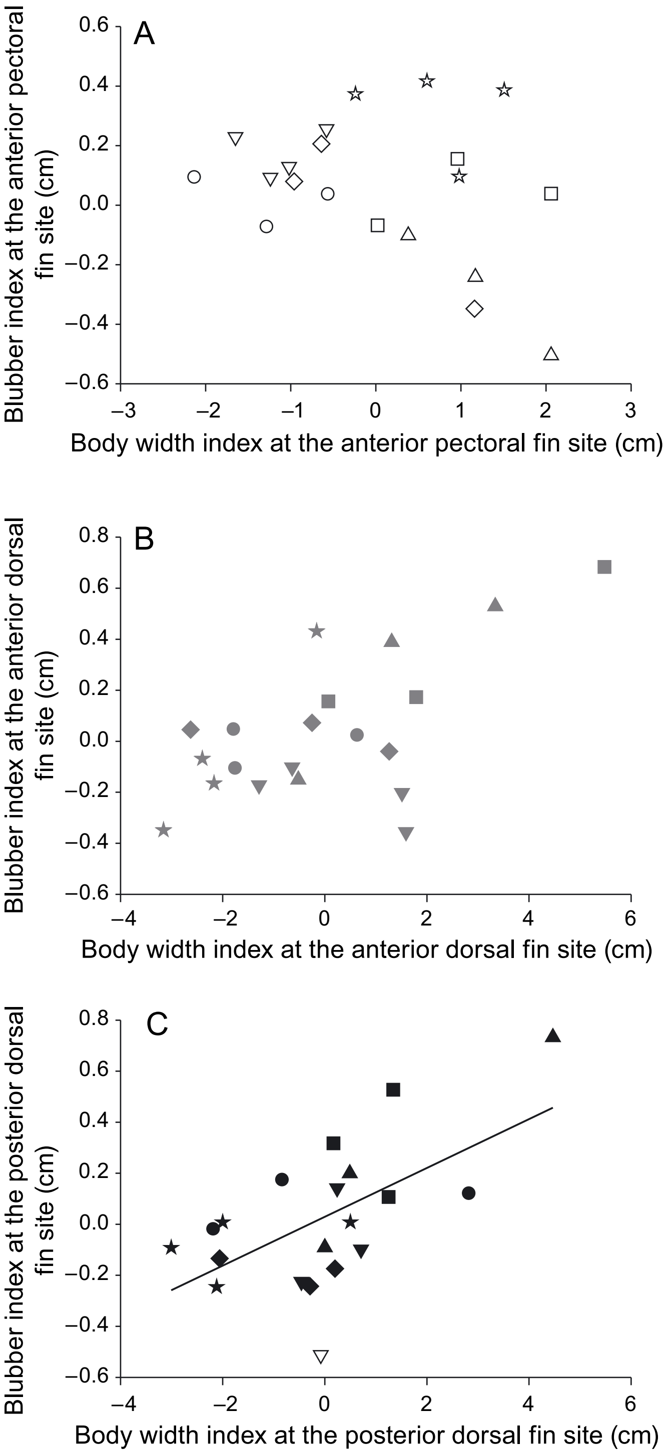

Fig. 5. Blubber index in relation to body width index at the (A) anterior pectoral, (B) anterior dorsal, and (C) posterior dorsal fin sites of pilot whales. Each individual whale is represented by a unique symbol colored white for the anterior pectoral (A), gray for the anterior dorsal (B), and black for the posterior dorsal (C) fin sites. The only relationship where there was no effect of individual on slope and/or intercept was for the posterior dorsal fin site; thus, data were combined across individuals, and this relationship is shown by the black line ($r^2 = 0.36$). See Table 3 for statistics

Table 3. Statistics for the 3 sites where photogrammetric body widths of short-finned pilot whales were measured in relation to the underlying blubber thickness and body girth at that site, as well as body mass (overall body condition). The variables were adjusted for body length as described in Sections 2.5 and 2.6, and different models were compared using Akaike's information criterion corrected for small sample size (AICc; as described in Section 2.7) to determine if model fit improved with inclusion of differences in slope and/or intercept by individual

	Individual important?	Slope	p	AICc with individual	AICc without individual
Photo width index versus blubber index (Fig. 5)					
Anterior pectoral fin	Intercept, not slope	–0.09	0.031	–12.63	1.98
Anterior dorsal fin	Intercept and slope	0.07	0.119	–4.82	1.24
Posterior dorsal fin	No	0.10	0.005	12.65	2.61
Photo width versus girth (Fig. 6)					
Anterior pectoral fin	No	3.65	<0.001	140.77	143.62
Anterior dorsal fin	Intercept, not slope	2.92	<0.001	124.77	130.79
Posterior dorsal fin	No	3.22	<0.001	130.15	131.25
Photo width index versus mass index (Fig. 7)					
Anterior pectoral fin	Intercept, not slope	9.9	0.240	186.5	201.3
Anterior dorsal fin	No	12.5	0.004	183.6	191.9
Posterior dorsal fin	Slope, not intercept	18.1	0.003	180.0	189.5
Photo width:length ratio versus mass index (Fig. 8)					
Anterior pectoral fin	Intercept, not slope	50.60	0.973	177.55	201.70
Anterior dorsal fin	Intercept, not slope	1495.66	0.195	176.71	200.81
Posterior dorsal fin	Intercept, not slope	3105.06	0.050	173.87	198.52

Body mass of free-ranging cetaceans is often unknown. To provide an application for use in the field, we examined how parameters measured from an overhead photograph (i.e. body width and body length) can predict mass index. Mass index was positively correlated with the photographic body width: length ratio at all 3 sites, but this relationship was only significant for the posterior dorsal fin site using a $p \leq 0.05$ criterion (Fig. 8). Model fit was improved with individual estimates of intercept, but not slope, for all 3 sites (Table 3). Across all whales and sample intervals, on average body width measured at the anterior pectoral fin, anterior dorsal fin, and posterior dorsal fin sites were at approximately 17, 28, and 47% of body length from the rostrum. Combined, our results indicate that measuring body width at approximately mid-body length and dividing that value by body length provides a reliable and sensitive proxy to monitor real changes in body condition of free-ranging pilot whales.

4. DISCUSSION

Conventional aircraft and unmanned aerial vehicles have been used in photogrammetry methodologies to assess the body condition of free-ranging cetaceans and offer a promising means of tracking the health of individuals and populations through time (i.e. Perryman & Lynn 2002, Suydam 2009, Durban et al. 2016). The majority of these efforts have focused on mysticetes (i.e. C. Miller et al. 2012, Christiansen et al. 2016). For the first time, here we (1) validated the underlying assumptions of this approach: variations in photogrammetric body width (across individuals and within individuals) correspond with actual variations in the underlying blubber thickness at those sites and variation in body mass, (2) demonstrated that photogrammetry is a reliable tool to monitor subtle changes in body condition in smaller-bodied cetaceans that are not fasting, and (3) showed that the site at which body width is measured as a proxy for overall body condition is extremely important. The region of the body where body width is measured should be from an area where body contours are not occluded by waves generated by swimming, and it must align with a region of the body where blubber is metabolically active, such that blubber thickness changes in accordance with variations in body mass.

Free-ranging long-finned pilot whales showed seasonal changes in body girth (anterior girth at the axilla, mid-girth anterior to dorsal fin, and posterior to dorsal fin), blubber thickness, and lipid storage (fat deposits around visceral organs and in the muscle and blubber; Lockyer 1993). These pilot whales had

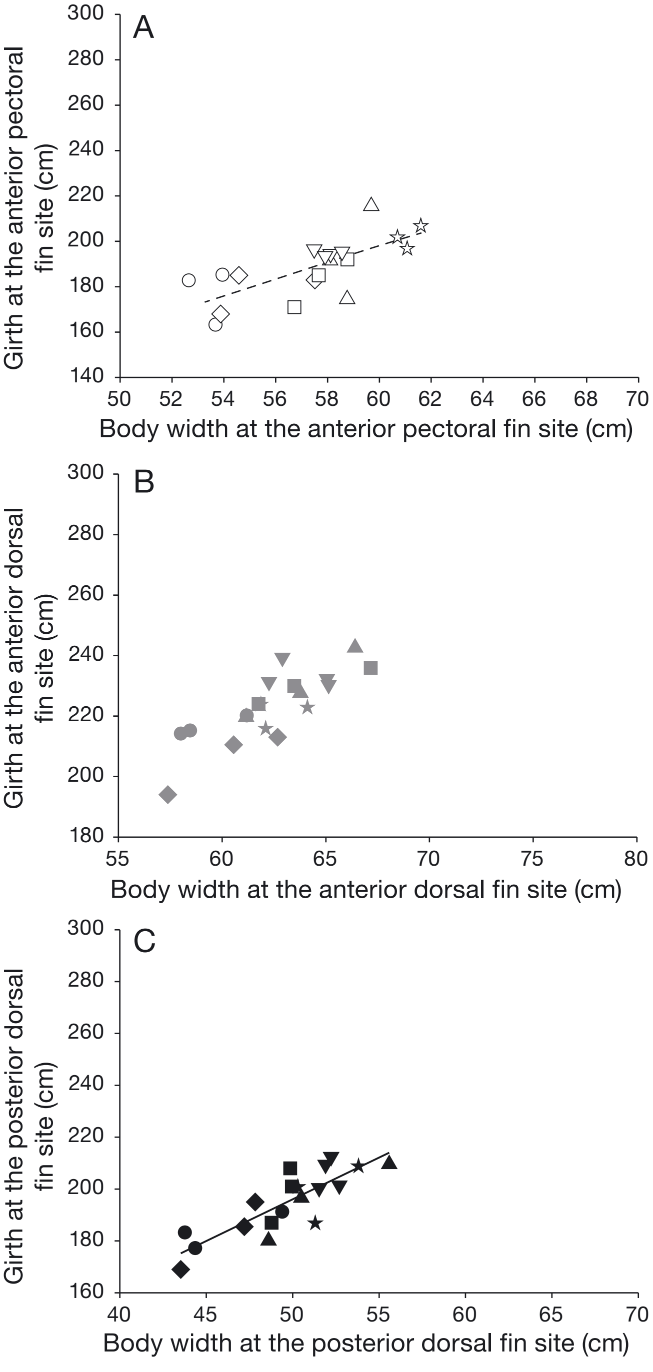

Fig. 6. Body girth in relation to body width at the (A) anterior pectoral, (B), anterior dorsal, and (C) posterior dorsal fin sites of pilot whales. Symbols as in Fig. 5. For 2 of the 3 sites there was no effect of individual on slope and/or intercept; thus, data were combined across individuals for the relationships at these 2 sites: anterior pectoral (dashed black line; $r^2 = 0.51$) and posterior dorsal (solid black line; $r^2 = 0.71$) fin sites. See Table 3 for statistics

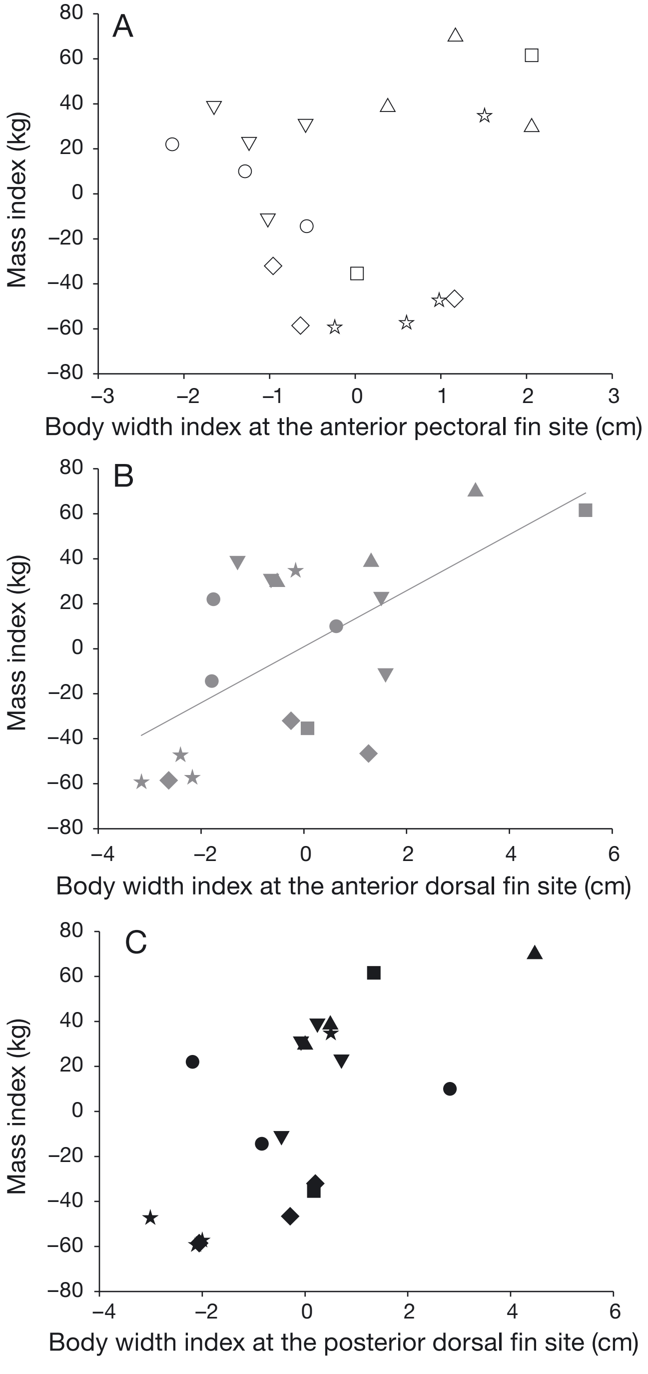

Fig. 7. Mass index in relation to body width index at the (A) anterior pectoral, (B) anterior dorsal, and (C) posterior dorsal fin locations of pilot whales. Symbols as in Fig. 5. The only relationship where there was no effect of individual on slope and/or intercept was for the anterior dorsal fin site; thus, data were combined across individuals, and this relationship is shown by the solid gray line ($r^2 = 0.40$). See Table 3 for statistics

greater body girths in winter and spring associated with a fattening period in winter and spring when water temperatures were cooler, compared to summer when water temperatures were warmer (Lockyer 1993). Similarly, over the course of our study the pilot whales had variable body conditions (Table 2)

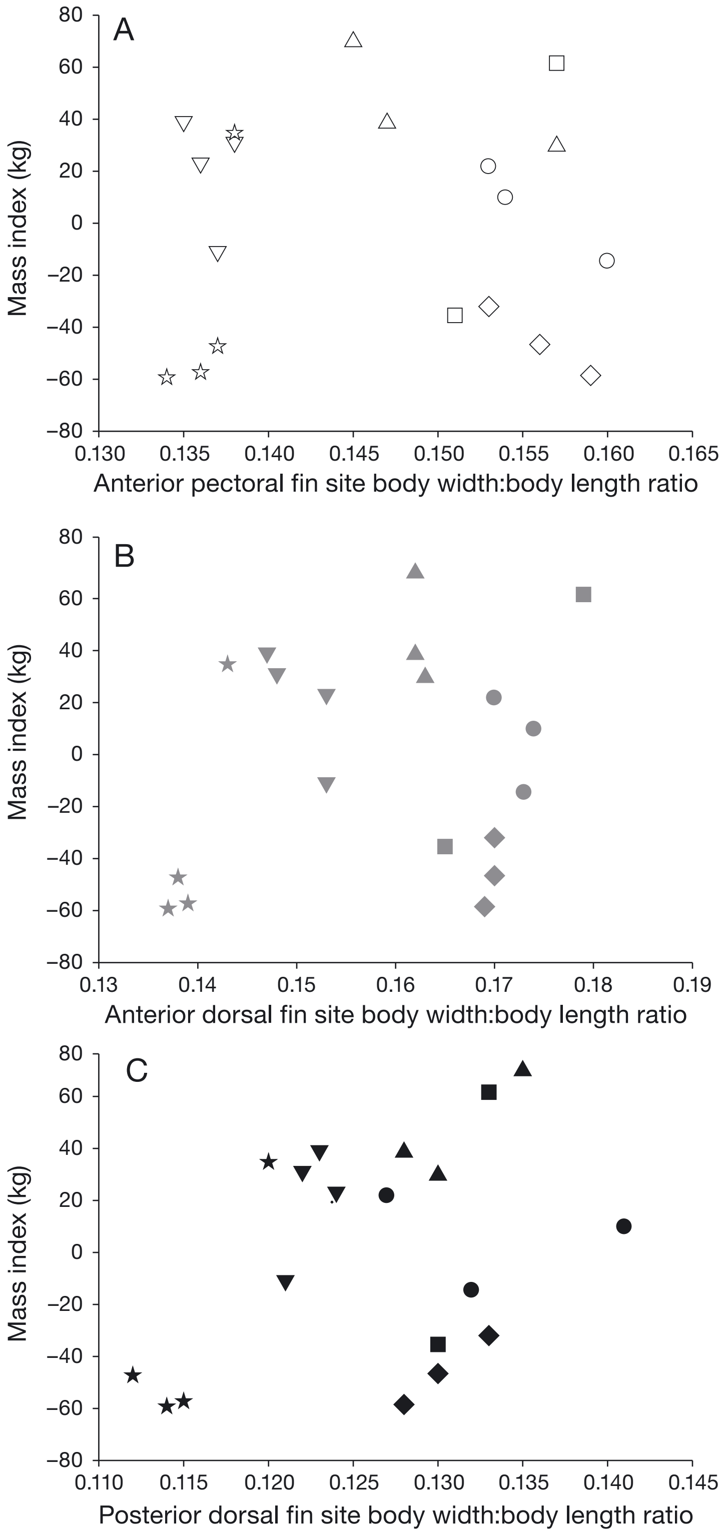

Fig. 8. Mass index in relation to body width divided by body length at the anterior pectoral (A), anterior dorsal (B), and posterior dorsal (C) fin sites of pilot whales. Symbols as in Fig. 5. The intercept for the relationship varied across individuals for each of the 3 sites, but the slopes were not impacted by individual at any of the sites. See Table 3 for statistics

that could have been associated with the variations in the water temperature in their pools. Across individuals and sampling intervals, body mass varied by 1.8 times from the lightest to heaviest measurements. Girth, the underlying blubber thickness, and body width measurements also varied. The controlled experimental design of this study allowed us to discern heterogenous changes in blubber thickness, body girth, and body width along the length of the body. Blubber thickness varied the most at the posterior dorsal site, by 1.7 times from the thinnest to thickest measurement. This compares to 1.5 times for blubber thickness measured at both the anterior pectoral fin and anterior dorsal fin site. Accordingly, body width measured from overhead photographs varied the most at the posterior dorsal fin site (48 % of body length from the rostrum), 1.3 times from the narrowest to widest measurement. Meanwhile, body width at both the anterior pectoral fin site and anterior dorsal fin sites (17 and 27 % of body length from the rostrum, respectively) varied by only 1.2 times.

Previous investigations have shown that intraseasonal variations in the body width of baleen whales are also heterogeneous. For example, a cross-sectional study of humpback whales at a breeding/resting ground showed that mature whales had the highest variations in body width at a location around 50–65 % of body length (from the rostrum); meanwhile the head (20–25 % of body length) and lower section of the peduncle (>80 % of body length) showed no significant variation in body width over the season (Christiansen et al. 2016). Likewise, lactating humpback whales (Christiansen et al. 2016) and lactating southern right whales (C. Miller et al. 2012) showed changes in body width between 35–80 % and 40–80 % of body length (from the rostrum), respectively. The disparate changes in body width along the length of the body for both baleen whales and pilot whales undoubtedly reflects regional variations in the function of blubber. Blubber in marine mammals not only acts as an energy reserve; it also serves to streamline the body, insulate the core, and adjust buoyancy (Ryg et al. 1988). For mysticetes, Christiansen et al. (2016) suggested that blubber serves as an energy reserve in the regions where body width changed (thoracic–abdominal region), while blubber in the regions where body width did not change (head and peduncle regions) serves more of a structural role (i.e. throat grooves at the head and streamlining of the tailstock in humpback whales).

Topographical variations in the thickness and histological and biochemical properties of the blubber along the length of the cetacean body support the notion that blubber has specific localized functions. Blubber in the dorsal flank of female fin whales *Balaenoptera physalus* increases in thickness by 25–45% during pregnancy and is depleted during lactation (Lockyer 1986). There is also greater thickening of the blubber in the thoracic abdominal region of minke whales *B. acutorostrata*, and the blubber in this region has higher lipid concentrations (Niæss et al. 1998). Higher lipid reserves in the thoracic abdominal region have also been observed for fin (Lockyer 1987, Christiansen et al. 2013) and sei *B. borealis* (Lockyer et al. 1985) whales, and it has been noted that female fin whales primarily mobilize lipids from the blubber in the dorsal flank region (Lockyer 1986). Odontocetes show similar patterns. The greatest blubber depths were observed in the region immediately posterior to the dorsal fin ridge in beluga whales (Doidge 1990, Cornick et al. 2016) and in the thoracic abdominal regions of finless porpoises *Neophocaena asiaeorientalis* (Zeng et al. 2015), harbor porpoises *Phocoena phocoena* (Koopman 1998), and sperm whales (Lockyer 1991). Blubber thickness in this region also changes most dramatically, as in beluga whales fattening in the fall (Cornick et al. 2016) and in harbor porpoises starving (thorax blubber of starving harbor porpoises is only 50–60% of the thickness of healthy animals; Koopman et al. 2002). The composition of the blubber in the thoracic region, such as elevated lipid concentration as observed in sperm whales (Watanabe & Suzuki 1950), as well as the stratification of fatty acids and number and size of adipocytes as observed in healthy versus starving harbor porpoises (Koopman et al. 1996, 2002), further indicates that blubber in the thoracic region serves as energy storage. In contrast, very little blubber was lost from the tailstock in starving porpoises, and the adipocytes in the blubber in this region were uniform across starving and healthy animals (Koopman et al. 1996, 2002, Koopman 1998).

Across the mysticete and odontocete species studied to date, blubber of the thorax appears to serve as the site of lipid deposition and mobilization, while blubber of the tailstock seems to be metabolically inert and is likely important for structural, streamlining, and locomotion functions. Given the topographic variation in the function of blubber along the length of the cetacean body, body width measurement sites used in the photogrammetric method for assessing body condition of free-ranging cetaceans must correspond to a region of the body where blubber serves as an energy reserve. Indeed, Lockyer et al. (1985) stated that to assess body condition it is preferable to measure blubber thickness at sites where it is most variable. Christiansen et al. (2016) recognized this as a factor to consider when using photogrammetry to monitor changes in body condition of baleen whales and recommended calculating the surface area of the whale showing at the water's surface to circumvent the issue of inadvertently measuring body width at a location that may vary little in relation to body condition. For mysticetes, this seems practical. They are comparatively large, slow-swimming animals, so the body contour along the peduncle is crisp for photogrammetric measurements. A validation study like this one is also impractical for mysticetes, thus measuring total surface area ensures that the region of the body that responds to varying energetic demands is captured in the analyses. Conversely, this approach is impractical for smaller-bodied, faster-swimming odontocetes because even in the most controlled environment it was difficult to capture photographs where the body contours of the peduncle were not occluded by waves (Fig. 2).

Given this constraint, we recommend measuring one body width at the site along the body where blubber thickness is reliably known to change the most in relation to periods of fattening and thinning. Our investigation showed that body widths measured at the anterior pectoral, anterior dorsal, and posterior dorsal fin sites were positively correlated with the tape-measured girths at the corresponding site, as would be expected (Fig. 6). Yet, once the condition metrics were corrected for body length (i.e. width index, blubber index, mass index), changes in body width at the 3 sites analyzed in this study were not always positively related, or significantly related, to changes in the underlying blubber thickness at the corresponding site (Fig. 5) or changes in overall body condition, body mass (Fig. 7). Indeed, amongst the 3 sites where body widths could be measured, only the posterior dorsal fin site had a significant and positive relationship with both blubber index (Fig. 5, Table 3) and mass index (Fig. 7, Table 3). These results suggest that, of the body width measurements taken in this study, body width just posterior of the dorsal fin is the most reliable indicator of the overall body condition of short-finned pilot whales.

To make our results applicable in the field, we needed to identify a metric that could predict body condition (mass index), since the body masses of free-ranging animals are unknown. For non-reproductive mature and sub-adult male and female pilot whales, posterior dorsal fin body width divided by body length was identified as the only measurement that reliably predicted mass index (Fig. 8), and this metric offers a promising tool to monitor the body condition of other free-ranging odontocetes. This result is in agreement with Lockyer (1993), who found that body length and the mid-body girth measurement combined strongly correlated with the body weight of free-ranging pilot whales, and that the addition of a second or third girth measurement as a factor(s) did not improve the predictive power of the relationship. Admittedly, some species may deviate from the generalized observation that blubber in the thorax serves as the energy reserve. For example, the number of adipocytes and blubber lipid content in striped dolphins *Stenella coeruleoalba* increased from dorsal to ventral positions (Gómez-Campos et al. 2015), suggesting that blubber in the ventral region ('belly') functions as energy storage, and it is unclear if blubber retention and utilization in a ventral site will be detectable in dorsal body width measurements taken from overhead photographs. It is unfortunate that Gómez-Campos et al. (2015) did not comment on differences in blubber histochemistry along the length of the dolphins, from beak to peduncle.

In conclusion, we demonstrate that subtle changes in the body width of smaller-bodied odontocetes that are not fasting are detectable when using photogrammetric methods, and we provide the first validation of the key assumption of the photogrammetric method, i.e. that changes in width at key locations along the body reflect changes in the underlying blubber layer at those sites that are in accordance with changes in body mass. Based on our current knowledge, we recommend measuring body width at about the mid-length of the animal and dividing this value by body length to get an index of condition. Testing the application of this method on pilot whales is particularly timely because of the concerns associated with the disruptions of foraging behavior by sonar operations for this species (i.e. Rendell & Gordon 1999, Sivle et al. 2012, Antunes et al. 2014) as well as other cetaceans (i.e. Tyack et al. 2011, Goldbogen et al. 2013, Miller et al. 2014). Additional research is warranted to ascertain if body width measurements about midway along the length of the body are reliable indicators of overall body condition in other odontocete species with diverse morphologies and phylogenies.

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