Marón Carina (Orcid ID: 0000-0003-3647-3355)
Sironi Mariano (Orcid ID: 0000-0003-3647-3355)
Rowntree Victoria (Orcid ID: 0000-0001-6153-8312)

[5005]-
Received: 8 June 2020 | Accepted: 19 March 2021

Running head: MARÓN ET AL.

ARTICLE

Patterns of blubber fat deposition and evaluation of body condition in growing southern right whale calves (*Eubalaena australis*)

Carina F. Marón[1,2] | María Carla Lábaque[1,3,4] | Lucas Beltramino[5] | Matías Di Martino[5] | Lucía Alzugaray[5] | Marcos Ricciardi[2] | Alejandro A. Fernández Ajó[2,6] | Frederick R. Adler[7] | Jon Seger[7] | Mariano Sironi[2,5,8] | Victoria J. Rowntree[2,5,7,9] | Marcela M. Uhart[5,10]

[1] Cátedra de Ecología, Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, Córdoba, Argentina

[2] Instituto de Conservación de Ballenas, Ciudad Autónoma de Buenos Aires, Argentina

[3] Instituto de Investigaciones Biológicas y Tecnológicas (IIByT), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Córdoba, Argentina

[4] Instituto de Ciencia y Tecnología de los Alimentos (ICTA), Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, Córdoba, Argentina

[5] Southern Right Whale Health Monitoring Program, Puerto Madryn, Argentina

[6] Center for Bioengineering Innovation, Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona

[7] School of Biological Sciences, University of Utah, Salt Lake City, Utah

[8] Cátedra de Diversidad Biológica IV, Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, Córdoba, Argentina

[9] Whale Conservation Institute/Ocean Alliance, Gloucester, Massachusetts

[10] Karen C. Drayer Wildlife Health Center, School of Veterinary Medicine, University of California – Davis, Davis, California

Correspondence

Carina F. Marón, Cátedra de Ecología, Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, 299 Vélez Sársfield Avenue, Córdoba 5000, Argentina.

Email: carimaron@gmail.com

Abstract

Marine mammals rely on blubber mainly for energy storage, buoyancy, and streamlining. Mysticetes are born with a relatively thin fat layer that grows rapidly during nursing. However, little information on blubber deposition patterns is available for baleen whale calves. We measured blubber thickness at nine body locations in 350 southern right whale (*Eubalaena australis*) newborn to 4–6-month-old calves that died on the Península Valdés (Argentina) calving ground from 2003 to 2019, to document changes in blubber thickness with growth. Additionally, we looked for differences in blubber thickness and lipid content of the outer/superficial blubber in calves that died in years with high (2003, 2005, 2007–2013) and low calf mortality (2004, 2006, 2014–2019) to test whether the former were suffering from gross nutritional stress. Blubber thickness increased at all body locations with calf length. Along the cranio-caudal axis, blubber increased in the dorsal and ventral planes, but decreased laterally towards the peduncle, possibly to improve streamlining. We found no difference in blubber thickness and lipid content between high and low mortality years, suggesting that individuals were not undernourished. This is the first study to describe progressive increases in calf blubber during growth and contributes knowledge to right whale health and ontogeny.

KEYWORDS

blubber thickness, growth, health, lipid content, ontogeny, Península Valdés calving ground

1 | INTRODUCTION

Adipose tissue is an important energy reservoir in mammals (Dugail & Guerre-Millo, 2009; Pond, 1978). Blubber, a subcutaneous layer composed of fat cells and collagen, is the most important storage of energy reserves in marine mammals along with a number of other functions, including providing insulation and buoyancy (Kvadsheim et al., 1996; Ryg et al., 1988; Struntz et al., 2004; Toedt, 2001), and maintaining the hydrodynamic shape of the body (Lockyer et al., 1985; Pabst et al., 1999; Parry, 1949; Pond, 1978). In baleen whales, calves are born with a relatively thin blubber layer but experience fast growth during nursing. In their first months of life, neonates show an intensive increase in body width that suggests rapid fat deposition (Christiansen et al., 2016, 2018).

Successive blubber thickness measurements can be used to detect patterns of fattening and growth in young calves (Christiansen et al., 2018; Miller et al., 2011). However, since blubber is not homogeneously distributed throughout the body of cetaceans, measurements should be taken at multiple body locations. In mysticetes, the posterior (caudal) region of the body represents an important fat storage area with the thickest blubber layers recorded at the dorsal- and ventral-posterior regions (Lockyer & Waters, 1986; Lockyer et al., 1985; Næss et al., 1998; Slijper, 1948). The posterior-lateral blubber, however, tends to decrease when reaching the caudal region, possibly to help streamline the whale's body (Lockyer & Waters, 1986; Lockyer et al., 1984; Næss et al., 1998; Reeb et al., 2007).

Southern right whale (*Eubalaena australis*) calves are born in winter and depend exclusively on maternal reserves for development and growth (Christiansen et al., 2018). In the southern right whale population off the coast of Península Valdés, Argentina, calves are primarily born in August (Whitehead & Payne, 1981) and nurse for a period of 2–3 months at this calving ground (Thomas & Taber, 1984). During this time, calves grow at a rate of approximately 3.5 cm/day (Whitehead & Payne, 1981) increasing from an average body length of 5–5.5 m to a maximum of ~9 m (McAloose et al., 2016; Whitehead & Payne, 1981). High calf mortality events that have occurred at Valdés in some years from 2003 to 2013 (at least 607 deaths; Rowntree et al., 2013), offer an opportunity to determine patterns of fattening along different planes of the calf's body during successive developmental stages, information that is scarce for the young of most baleen whale species. Blubber thickness measurements from a large number of dead calves have been taken continuously since 2003 (the beginning of the high calf mortality events) to better understand patterns of fat deposition with calf growth and development.

In addition, blubber thickness and lipid content in blubber can be used to assess body fat condition in whales since these indicators change with the nutritional status of individuals (Bradford et al., 2012; Gulland & Hall, 2005; Koopman et al., 2002; Lockyer, 2007; Lockyer & Waters, 1986; Miller et al., 2011, 2012). Although the main causes for recent high calf mortality events in the Valdés right whale population have not yet been identified (International Whaling Commission, 2018), poor nutritional state of mothers has been proposed as a potential contributor (International Whaling Commission, 2011; Rowntree et al., 2013; Sironi et al., 2016; Thomas et al., 2013; Uhart et al., 2009). Nutritional stress could affect calf survival since there is evidence that mature females increased the proportion of abnormally long calving intervals in this population following years of low Antarctic krill abundance (*Euphausia superba*), one of the whales' prey (Leaper et al., 2006). Assessing blubber thickness measurements and lipid content in calves that died during high and low mortality years at Valdés allows us to evaluate their body condition, and indirectly that of their mothers, through time.

Here, we studied changes in blubber thickness at different body locations (dorsally, ventrally, and laterally along the axillary, umbilical and anal girths) during calf growth (calf length and age) to assess patterns of fattening. We determined whether blubber thickness was affected by sex, state of carcass decay, and the two areas where most strandings occur at Península Valdés (Golfo Nuevo vs. Golfo San José). Finally, and controlling for calf length and state of decay, we compared blubber thickness and lipid content in the outer blubber (close to the skin) in calves that died in the period 2003–22019 to evaluate whether the condition of their blubber reserves decreased during years of high calf mortality.

2 | MATERIALS AND METHODS

2.1 | Necropsies

Necropsies of southern right whale calves were conducted from June to December at Península Valdés (Golfo Nuevo and Golfo San José) from 2003 to 2019 by the Southern Right Whale Health Monitoring Program (SRWHMP) following the SRWHMP necropsy protocol (Chirife et al., 2014). Stranded calves were newborns (1 day old), neonates (<2 weeks old), or calves <4–6 months old (McAloose et al. 2016; Sironi et al., 2018; Uhart et al., 2008, 2009). The SRWHMP recorded total length, blubber thickness, carcass decomposition, and sex of individuals, along with date of necropsy and stranding area (Table S1). Blubber samples were collected primarily along the dorsal plane of the body for lipid content analysis.

2.2 | Length measurements and age classes

Length from snout tip to fluke notch was measured in meters with a measuring tape. Measurements were taken in a straight line (not following the curve of the body) independently of the whale’s stranding position.

We used dead calf length as a proxy for age. Three age class categories were determined using length measurements and a combination of morphological characteristics: (1) newborn and neonate (open or healing umbilicus, orange cyamids on cheeks, <5 m); (2) young calf (healed umbilicus, orange cyamids on cheeks, 5–7 m); and (3) old calf (healed umbilicus, white cyamids on callosities, 7–9 m); (see McAloose et al., 2016 for more morphological details).

2.3 | Blubber thickness measurements

Blubber thickness in dead calves was determined in situ at three body girths when allowed by their stranded position and state of decay. Blubber thickness was measured in centimeters using a metal ruler at dorsal, lateral, and ventral sites along the axillary (1), umbilical (2), and anal (3) girths (nine measurements in total; Figure 1). First, we made a longitudinal cranial-caudal cut and then, three lateral cuts at the axillary (measured at the posterior insertion of the flipper), umbilical, and anal girths. After each lateral cut, we measured blubber thickness at the dorsal, lateral, and ventral sites. Dorsal or ventral blubber thickness was not determined in individuals that stranded in a dorso-ventral position (with their backs on the sand) or in a ventro-dorsal position (with their bellies on the sand), respectively. We measured blubber thickness at all sites when the whales stranded in a lateral (left or right) position. Blubber thickness was measured perpendicularly from the dermis to the basal hypodermis, and the upper epidermal layer was not included in the measurements (for definitions of the integument of *E. australis* see Reeb et al., 2007). Blubber thickness was measured only when blubber was not detached from the skin. We avoided measuring blubber thickness in areas of the whale's back affected by kelp gull (*Larus dominicanus*) lesions since the wounds can extend from the skin to the blubber layer below, and thus would affect our measurements (Marón, Beltramino, et al., 2015; McAloose et al., 2016).

2.4 | **Carcass decomposition**

A necropsy carcass condition code was assigned to each calf based on the state of decomposition of tissues and organs. Given inherent carcass and observer variations, some or all descriptors were used to assign decomposition condition, following Geraci & Lounsbury (2005). Condition code 2 included fresh dead calves with normal appearance, not bloated, fresh smell, minimal drying or wrinkling skin, little scavenger damage, slightly dry eyes and mucous membranes, no protrusion of tongue or penis and internal organs conserved. Condition code 3 included dead calves with an intact carcass but bloated, mild odor, wrinkled and/or detached skin, possible scavenger damage, sunken or missing eyes, dry mucous membranes, tongue or penis protrusion, and most internal organs conserved. Condition code 4 included dead calves with an intact carcass but internally collapsing, strong odor, skin sloughing and sometimes detached, possible scavenger damage, easy detachment of muscle tissue, and most internal organs liquefied. Variations observed in blubber were as follows; calves in condition 2 had a very white-pinkish blubber with no odor and a soft structure; in condition 3, calves presented a white-yellowish blubber with mild odor, and in condition 4, blubber was white-brownish-greenish with strong odor, but remained attached to the skin and did not appear liquefied (it kept its structure). For blubber thickness measurements, we selected dead calves in conditions 2, 3 and 4. Decomposition can be heterogenic across the body; thus, condition 4 carcasses were only included when blubber was soft, still attached to the skin, maintained structure, and had a white-ish coloration. Carcasses in which blubber looked liquefied and with oil dripping from this layer were not measured. Also, calves that were in an intermediate condition between 3 and 4 (i.e., condition 3.5) were classified as condition 4 for simplification of the analysis. Blubber samples for lipid analysis were taken from dead calves in conditions 2 (*n* = 16, 27% of total) and 3 (*n* = 43, 73% of total).

2.5 | Blubber samples from dead calves for lipid content analysis

A full blubber sample (5 × 5 cm to 15 × 15 cm) with skin attached was collected from numerous dead calves that stranded in 2009–2012 and 2014–2016, and stored frozen at −20°C or −80°C in an airtight plastic bag until analysis (Table S2). Samples were used if they came from whales in condition codes 2 and 3 (fresh and moderate decomposition, Geraci & Lounsbury, 2005). We did not collect samples from condition 4 calves because lipid content decreases in the blubber of cetaceans at advanced states of decay (Borrell & Aguilar, 1990; Gauthier et al., 1997; Gulland & Hall, 2005). Samples were collected at different body locations but mostly from the dorsal anterior region of the calf’s body (81%) to make them comparable to blubber biopsy samples collected from living calves. For each frozen sample, a horizontal blubber core (0.8 cm in diameter × 4 cm long) was drilled at 1 cm below the beginning of the dermal layer. We removed the extremes of the core (which were in contact with the air and thus more prone to oxidation) and used a ~2 cm blubber sample for lipid content analysis. Blubber samples were only taken from the superficial or outer blubber layer (close to the skin) and not from the deeper layers to make them comparable to blubber biopsy samples collected from living calves.

2.5 | Lipid content analysis in living calves to compare with dead calves

Lipid content analysis in living calves was performed to determine whether lipid content values in the blubber from dead calves were affected by post-mortem conditions. Blubber biopsy samples from living calves were collected in 2016 at Golfo San José, Península Valdés, using darts propelled by a crossbow (Brown et al., 1991). All living calves that were biopsied were considered to be young or old calves (>6 m); newborns and neonates (<5 m) were not biopsied. Samples were taken dorsally, mainly at the mid-section of the body. The biopsy darts were fitted with tips 0.5 cm in diameter and 4 cm long and removed small samples of the outer blubber layer approximately 2–3 cm deep. Each blubber biopsy was placed in double sterile plastic bags and preserved wrapped in pantyhose in an insulated liquid nitrogen Dewar for up to 3 months until analysis. For lipid content analysis, we removed the epidermal and dermal layers of the sample using only the blubber.

2.6 | Lipid content

Procedures for preparation of blubber samples for lipid extraction were similar to those described by Borell and Aguilar (1990) and Ryan et al. (2013). Samples were weighed to approximately 0.5–1 g (dead calf samples) and 0.3–0.6 g (living calf biopsies) and placed in previously weighted paper envelopes in a Soxhlet apparatus with 150 ml *n*-hexane. Materials used during the analytical process (scalpel and forceps) were rinsed with *n*-hexane. The best extraction time was determined using blubber samples from dead calves in necropsy condition code 2 (fresh). Duplicates (*n* = 20) were tested using two extraction methods in a Soxhlet apparatus: (1) hexane for 6 hr and (2) hexane for 6 hr followed by soaking for 16 hr. Because we found no significant differences between the two extractions, method (a) was used for the remaining analyses of dead and living calf samples. After samples were washed for 6 hr in Soxhlet envelopes (~40 cycles), they were dried in a desiccator chamber for 24 hr until the solvent was fully evaporated. Dry envelopes were weighed, the envelope weight was subtracted, and the percentage lipid thus calculated gravimetrically by dividing total lipid weight by blubber wet weight. All lipid contents were expressed as a percentage of wet tissue weight.

2.7 | High and low mortality years

We defined “high mortality” and “low mortality” years in the 2000s to evaluate whether blubber thickness of calves decreased in high calf-mortality years when deaths could have been related to malnutrition. A current analysis of the observed number of dead calves is under preparation to define low mortality years and high mortality years in the period 1971–2019 at Península Valdés (Marón, Rowntree, et al., 2015). Briefly, we fitted an exponential curve to the number of dead calves from 1971 to 2013, assuming an annual growth rate of 6.8% (Cooke et al., 2003) and that the detection efficiency of dead calves by the SRWHMP was 1.75 times greater than the average efficiency during 1971–2002 (when the SRWHMP was not yet operational). Even with this generous assumption of improvement in detection of dead calves by the SRWHMP, calf deaths in 2003, 2005, and 2007–2013 were all significantly greater than expected (Marón, Rowntree, et al., 2015). The largest number of dead calves recorded in a low mortality year (2006) was 14 and the lowest number recorded in a high mortality year (2003) was 29 (Sironi et al., 2018; SRWHMP, unpublished data). Thus, for this study we defined low mortality years in the 2000s as the years when the number of dead calves was not found to be significantly greater than expected (2004, 2006, 2014–2019) and high mortality years as years when the number of dead calves was significantly greater than expected (2003, 2005 and 2007–2013).

2.8 | Statistical analyses

All blubber thickness comparisons were adjusted for calf length (covariate) because blubber thickness increases with calf age, as shown from results of ultrasound measurements in living southern right whales off South Africa (Miller et al., 2011). In addition to calf length, we included necropsy carcass condition as another covariate in all blubber thickness statistical analyses. Although all these models were run with calves in condition codes 2, 3, and 4, we repeated all comparisons excluding calves in condition code 4 and obtained similar results. Therefore, all results reported here include calves in all condition codes (2, 3, and 4). Linear regression models were used on each of the nine blubber measurements to determine how blubber thickness changes with calf length. To determine detailed changes in the patterns of fattening along the cranio-caudal axis of the calf’s body, and on the axillary, umbilical, and anal girths, we compared all blubber thickness measurements among calves of gradually increasing lengths through linear regression models and linear mixed effects models (lmer). The linear regression models were run with interaction between the measuring site (nine measurements in total; Figure 1) and calf length. The *p*-values reported in the Results correspond to the linear regression models that were checked for robustness with lmer, which in every case only increased the strength of results. Adjusting by length, we also ran linear models to evaluate whether blubber thickness varies with necropsy condition in calves (all models were run with and without interaction between length and necropsy condition) and then we contrasted all models using analysis of variance (ANOVA). Using calf length and necropsy carcass condition as covariates, linear models were also used to evaluate differences in blubber thickness of dead calves in relation to the following independent variables: calf sex, stranding area (Golfo Nuevo and Golfo San José), and low and high mortality years. Finally, linear models were used to assess whether the lipid content in the blubber of calves that died in high mortality years was significantly different from calves that died in low mortality years. To determine whether lipid content of blubber in dead calves was affected by different states of decomposition (condition code 2 and 3), sex, and stranding area we used linear regression models. All statistical analyses were conducted using R software version 3.5.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Blubber thickness in southern right whale calves

A total of 2,206 blubber thickness measurements at the dorsal, lateral, and ventral sites along the axillary, umbilical, and anal girths were taken in 350 calves that died at Península Valdés from 2003 to 2019 (Table S1). Of this total, 49% were females and 46% males (5% of unknown sex), 77% stranded in Golfo Nuevo and 23% in Golfo San José, and 62% were in an advanced decomposition state, 27% in moderate decomposition, and 9% were fresh (2% unknown). Over all calf ages, the smallest mean blubber thicknesses were recorded at the dorsal-axillary site (M = 4.39 cm) and at the dorsal-umbilical site (M = 5.33 cm) and the largest mean at the dorsal-anal site (M = 7.23 cm) and the ventral-anal site (M = 8.47 cm) (Figure 2). The minimum and maximum calf blubber thickness values were measured at the dorsal-axillary in a newborn (blubber thickness: 0.70 cm, calf length: 4.17 m) and the ventral-anal sites in a young calf (blubber thickness: 18.50 cm, calf length: 6.91 m).

3.2 | Blubber thickness changes with moderate carcass decay only in one measuring site

Controlling for calf length, carcass decomposition status had no detectable effect on eight blubber thickness measurements among calves of similar size (ANOVA, p = 0.25–0.88; Figure 3).

However, blubber thickness at the dorsal-umbilical site was lower among calves in condition code 3 compared to calves in condition 2 and 4 (ANOVA, $p = .05$). As a result, the analyses described below were adjusted in all cases by calf length and state of decay.

3.3 | Blubber thickness increases with calf length and age

Both length and at least one blubber thickness measurement were recorded in 350 dead calves. Calf length ranged from 3.15 to 8.42 m (Table S1). Blubber thickness of dead calves increased with length in all nine blubber thickness measurements at the dorsal, lateral, and ventral sites along the axillary, umbilical, and anal girths (regression, $0.46 \leq R^2 \leq 0.63$, all p-values < .001).

From a total of 350 dead calves, 25% were newborns or neonates, 62% were young calves, and 13% were old calves (Table S1). In newborns and neonates, blubber thickness averaged from 2.96 cm at the dorsal-axillary site to 6.40 cm at the ventral-anal; in young calves, from 4.30 cm at the dorsal-axillary site to 8.39 cm at the ventral-anal; and in old calves, from 8.62 cm at the dorsal-axillary site to 12.38 cm at the ventral-anal (Table 1). Between newborns/neonates and young calves, blubber increased from 31% to 59% at each measuring site. Moreover, between young and old calves, the increase was more pronounced ranging from 48% to 100% (Table 1). Dorsal-axillary, dorsal–umbilical, and lateral-axillary were the sites where the largest increments occurred in growing calves. Lateral- and ventral-anal were the sites with the smallest increments.

3.4 | Calves acquire a more streamlined body shape with length

Along the cranio-caudal axis, blubber thickness of calves of increasing lengths augmented dorsally and ventrally (Figures 2 and 4). Blubber at the dorsal-axillary site was thinner than the other two more caudal dorsal sites, but this difference was only significant for dorsal-axillary versus dorsal-anal comparison (regression, $p = .003$). Similarly, blubber at the ventral-axillary site was thinner than the other two more caudal ventral sites, but this difference was significant for ventral-axillary versus ventral-umbilical sites (regression, $p = .04$). Laterally, blubber was thinner at the lateral-anal site (close to the peduncle) than at the lateral-axillary (close to the head; regression, $p = .05$) and the lateral-umbilical (center; regression, $p = .006$) sites, favoring streamlining. This difference is evident in calves longer than 6 m (Figure 4).

On the axillary and umbilical girths, the increase in blubber thickness with calf length was greater on the lateral and ventral surfaces (Figure 5). Axillary, blubber at the dorsal site was thinner than blubber at the lateral and ventral sites, but this difference was only significant for the dorsal-axillary versus lateral-axillary comparison (regression, $p < .001$). Similarly, on the umbilical girth, blubber at the dorsal site was thinner than blubber at the lateral and ventral sites, but in this case both differences were significant (regression, dorsal-umbilical versus lateral-umbilical comparison: $p = .002$, dorsal-umbilical versus ventral-umbilical comparison: $p = .004$). For the most caudal girth, the anal girth, blubber was thinner at the lateral-anal site than at the upper dorsal and lower ventral sites, but these differences were not found to be statistically significant in any case.

3.5 | Blubber thickness differs between stranding areas but not between sexes

Of the 350 calves included in this study, 269 died in Golfo Nuevo (length range: 3.15–8.32 m; 51% females, 45% males, 4% unknown sex) and 81 died in Golfo San José (length range: 3.78–8.42 m; 44% females, 52% males, 4% unknown sex). Controlling for length and necropsy condition, calves that died in Golfo Nuevo had thicker blubber than those dying in Golfo San José in all nine blubber thickness measurement sites. From these nine measurements, six sites were significantly different (lateral-axillary, -umbilical, and -anal, ventral-axillary, -umbilical, and -anal; regression, $p = .001–.04$).

Sex had no detectable effect on blubber thickness of dead calves in all the nine sites along the axillary, umbilical, and anal girths (regression, all p = .14–.83).

3.6 | Blubber thickness does not change between calves that died in low and high mortality years

Controlling for length and carcass condition, blubber measurements were similar between calves that died in high versus low mortality years at eight out of nine blubber sites (regression, p = .09–.81; Table 1). Calf blubber was thicker at the lateral-axillary site in high mortality years compared to low mortality years (regression, p = .02; Figure S1). Similar results were obtained when comparing within each age class separately (newborn/neonates and young calves; regression, p = .06–.84), except that blubber was thicker at the lateral-axillary site only for young calves in high mortality years (regression, p = .003). Old calves were excluded from these comparisons because of low sample size in high mortality years for all measuring sites (sample size ranged from one to three; Table 1).

3.7 | Similar lipid content values in living and dead calves and in calves that died in low and high mortality years

Lipid content in the outer blubber was analyzed in 59 calves that died at Península Valdés in the period 2009–2012 and

2014–2016 (*M* ± *SD*, 75.69 ± 5.21% wet weight), and in 16 living calves biopsied in 2016 (76.72 ± 5.18% wet weight). Values in blubber from dead calves were within the range of lipid contents measured in biopsy samples from living calves (ANOVA, $p = .49$); thus, lipid content values in dead calves were representative of premortem conditions.

Adjusting by length, lipid content in blubber of dead calves was not found to vary significantly between years of low and high calf mortality (regression, $p = .24$). Similar results were found for lipid content versus state of decomposition (fresh or moderate decomposition, regression, $p = .36$), sex (regression, $p = .84$), or stranding area (regression, $p = .62$). However, as dead calves increased in length their levels of blubber fat declined (regression, $p < .001$). Lipid content also decreased with increasing blubber thickness measurements at all body locations, but this difference was significant only for the ventral-axillary site (regression, $p = .001$).

4 | DISCUSSION

This is the first ontogenic study to characterize progressive changes in blubber thickness in a large number of dead whale calves during successive growth stages at their calving ground. As expected, we found that blubber thickness increased with calf growth, yet these variations differed with location in the calf’s body, suggesting a selective pattern in fat deposition that favors the hydrodynamic shape of the body. We did not find differences in blubber thickness or in blubber lipid content that could associate high mortality years with a direct nutritional factor affecting blubber fat storage in calves. This implies that mechanisms other than limited accumulation of fat reserves in calves might have played a role in high mortality events.

Blubber thickness increases with growth in young cetaceans (Koopman, 1998; Lockyer, 1993; Miller et al., 2011; Struntz et al., 2004) because fat reserves are expected to increase with nursing. This is consistent with our findings for southern right whale calves ranging from newborn/neonates (<5 m) to calves up to 8.42 m that died at Península Valdés. The blubber thickness of these dead calves increased with length in a manner similar to that of dead (n = 5, <6 m) and living (n = 16) southern right whale calves off South Africa, measured by ruler and ultrasound methods, respectively (Miller et al., 2011; Reeb et al., 2007). Photogrammetric studies in southern right whales off Australia show that calf body widths increased proportionally as they grew, suggesting blubber accumulation with gradually increasing lengths (Christiansen et al., 2018). Blubber thickness at the lateral-anal site increased with length in southern right whales illegally caught in the 1960s, but few harvested individuals were calves (~8–9 m) and most were juveniles and adults (Tormosov et al., 1998). A positive linear relationship of dorsal blubber thickness (acoustic measurement) with body length was not found in living North Atlantic right whale calves (*E. glacialis*), but this result may differ with findings in southern right whales because of the small number of *E. glacialis* calves measured (n = 8) within a limited range of lengths (~8.5–10 m, Miller et al., 2011).

Blubber thickness changes with body location and age in calves. Fat is not equally distributed along the body of growing calves. Calves are born with the thinnest blubber located at the dorsal-axillary site. Blubber at this site increases rapidly throughout growth but remains the thinnest site even for older calves. The reason for this is unclear. A plausible explanation may be that blubber is thinner in certain areas to facilitate movement. Blubber surrounding the neck area might be thinnest in calves to allow more head flexibility during nursing. It could also be a consequence of the evolutionary history of Balaenidae rather than an adaptation to a specific physiological requirement. Conversely, calves are born with the thickest blubber located at the ventral-anal site which continues to be the deepest layer throughout growth along with the dorsal-anal site. The ventral- and dorsal-anal blubber are located near the peduncle, a location that has been proposed as an energy storage site in adult fin and sei whales (*Balaenoptera physalus* and *B. borealis*; Lockyer et al., 1985). Future studies should explore these hypotheses as plausible explanations for differential patterns of fat accumulation along the body of growing calves. Furthermore, blubber increments are more pronounced after calves exceed 7 m in length, i.e., when calves are older than 1–2 months. These increases are probably explained because calves start preparing for migration after their third month of life on the Valdés calving ground (Thomas & Taber, 1984). Developing deeper blubber layers around the body may enhance thermal insulation and buoyancy (Kvadsheim et al., 1996; Noren & Wells, 2009; Nousek-McGregor et al., 2014). High thermal and buoyancy demands may be imposed during migration to deeper and colder waters at the southern feeding grounds used by southern right whales (Zerbini et al., 2016).

Patterns of blubber distribution over the calf's body vary with growth. We found that dorsal and ventral blubber thickens towards the caudal region of the body, while lateral blubber thins towards the tail. A similar pattern of fattening was found by Reeb et al. (2007) in five southern right whale calves off South Africa and by Koopman (1998) in 11 harbor porpoises

(*Phocoena phocoena*) from North Atlantic waters. Our results support previous studies showing the role of blubber as a structural tissue that laterally streamlines the body of whales (Lockyer & Waters, 1986; Lockyer et al., 1985; Næss et al., 1998; Slijper, 1948) and thus improves propulsion (Hamilton et al., 2004; Pabst et al., 1999; Summers, 2001). We also found that blubber thickens dorso-ventrally along the axillary and umbilical girths, but decreases laterally along the anal girth, which is closer to the peduncle. Compared to the ventral blubber, dorsal blubber appears to be thinner in the anterior and midsection of the calf’s body (axillary and umbilical girths) but it appears to be similar along the caudal section (anal girth). The lateral blubber, however, tends to decrease along the caudal section creating a lateral compression on the tailstock.

Blubber thickness appears not to change with carcass decomposition except for one blubber measurement site taken dorsally along the umbilical girth. Most calves found dead at Valdés are in moderate to advanced state of decay (condition codes 3 and 4) because an unknown period (rarely hours, often days) passes between their deaths, their stranding on the beach, and the necropsy examinations (Uhart et al., 2008, 2009). Our findings suggest that blubber thickness measurements may not be affected greatly by the state of decay of calves, at least for individuals in conditions 2–4 (see Methods for definitions of states of decay 2, 3, and 4). Based on hundreds of necropsy examinations of dead calves at Península Valdés, blubber of calves seems to decompose more steadily than in larger whales. Thus, in most condition 4 calves the thickness and overall structure of the blubber layers are apparently preserved. These results may not be accurate for southern right whale adults in necropsy condition codes 3–4 or for other cetacean species. In adult whales, blubber probably decomposes more rapidly because of the greater thickness of the layer (e.g., in southern right whales, two to three times thicker than calves) which traps internal heat and accelerates decomposition (Cawthorn, 1997). Little is known about how states of decay affect blubber thickness in dead marine mammals. Gauthier et al. (1997) reported that the blubber thickness of a dead minke whale (*Balaenoptera acutorostrata*) did not seem to vary when comparing samples taken 24 hr after death to samples taken 1 month after death. However, lipid content of blubber, which seems more sensitive to degradation (Borrell & Aguilar, 1990; Gulland & Hall, 2005) decreased significantly during that same period. This may indicate that while the fibrous structure of the blubber (connective tissue fibers) remains more stable during the first decomposition stages, lipids start to leach from the blubber layer more rapidly (Borrell & Aguilar, 1990; Gauthier et al., 1997). In this study we found no differences in lipid content of calves in fresh versus moderate state of decomposition (conditions 2 and 3), neither between dead calves and live-calf biopsy samples.

Blubber thickness appears to be similar in male and female calves. Sex has been shown to have a strong effect on the blubber reserves of adult living and dead whales (Lockyer, 1981, 1987; Lockyer & Waters, 1986; Miller et al., 2011; Pettis et al., 2004). But it has not previously been assessed in baleen whale calves and has been studied in only a few toothed whales (e.g., *Phocoena phocoena* and *Pontoporia blainvillei*; Caon et al., 2007; Lockyer, 1995). For instance, in the harbor porpoise, blubber is thicker in female neonates compared to males, maybe to favor female calf survival (Lockyer, 1995). Adult female baleen whales accumulate more blubber than adult males during certain phases of their reproductive cycles. These females had the thickest blubber prior to (Miller et al., 2011) and during pregnancy (Lockyer, 1981, 1987; Lockyer & Waters, 1986) compared to juveniles, adult males, or adult females in other reproductive stages (e.g., lactating females). These differential patterns of fattening were not detectable among calves of different sex in our study, an expected finding considering that sex may only influence blubber thickness in adult female mysticetes undergoing different reproductive stages (Miller et al., 2011).

Blubber appears to be similar overall in calves that died in low and in high mortality years. Moreover, lipid content in the outer blubber did not differ among calves that died in low or high mortality years. These findings are consistent with a previous study showing that the majority of calves that have died at Valdés do not present signs of debilitation or emaciation, regardless of annual mortality levels (McAloose et al., 2016). Although their results showed that bone marrow fat was overall low and that epicardial or perirenal atrophy of adipose tissue was commonly found in dead calves, this result is expected for their age range. In adult baleen whales, emaciation is evident through a reduction in dorsal blubber behind the blowholes that makes their scapulas appear protruded and the lateral flanks depressed (Bradford et al., 2008; Brownell & Weller, 2001; Moore et al., 2001, 2004). We did not observe either of these anatomical features in any of the calves. Our results are also consistent with a recent study that found no differences in the fatty acid profiles of living and dead calves in Península Valdés, which indicates no evidence of inefficient transfer of fatty acids from mothers to calves or variation in maternal diets. Also, another study in dead calves of this population showed stable levels of triiodothyronine (T3), a metabolic hormone that decreases under nutritional stress (Fernández Ajó et al., 2020). Notwithstanding, although we found no evidence of thinner blubber or less fat content in calves that died during high mortality years, a nutritional factor cannot be ruled out as a contributor to calf deaths in those years. Specifically, in this study the deeper blubber layers were not examined, which could be more metabolically active than the outer layers and could reflect more directly the nutritional status of calves as occurs for adult cetaceans of other species (Aguilar & Borrell, 1990; Koopman, 2007). Many other analyses, including ongoing behavioral (e.g., blow intervals in mothers and calves as a proxy for energy costs), nutritional (e.g., diet composition of mothers), and physiological (e.g., hormones related to nutritional stress in dead calves) analyses, along with photogrammetric studies, will supplement the findings presented in this study and allow for a better understanding of underlying morbidity/debilitating processes. To date, a principal cause/s of death for calves during high mortality years at Península Valdés have not been identified. Causes of death have been establish only for ~7% of over 200 calves through postmortem examination and pathogen testing (pneumonia, myocarditis, and meningitis, McAloose et al. 2016). Probably multiple processes have influenced calf mortality events.

Values of lipid content reported here in the outer blubber layer of calves are within the ranges found in adult fin, sei, and minke whales (Aguilar & Borrell, 1990; Gauthier et al., 1997). Lipid content can vary among blubber layers on whales of different age, sex, nutritional and reproductive status, i.e., stratification (Aguilar & Borrell, 1990, 1991; Evans et al., 2003; Koopman et al., 2002). In some adult baleen and toothed whales, blubber fat content is vertically stratified and the outer layer is more stable than the more active inner layer (i.e., lipid content in the outer layer is little affected by the whales' body condition thus it may function as a structural or thermoregulatory layer, instead, inner fat content changes in relation to nutritional or reproductive status and constitutes an energy reservoir for lipid deposition and mobilization; Aguilar & Borrell, 1990; Koopman, 2007). However, in adult fin whales, minke whales, white whales (*Delphinapterus leucas*), killer whales (*Orcinus orca*), common dolphins (*Delphinus delphis*), long-finned pilot whale (*Globicephala melas*), common bottlenose dolphins (*Tursiops truncatus)*, and Sowerby's beaked whales (*Mesoplodon bidens*) no significant differences were found in lipid content among blubber layers of adult whales (Aguilar & Borrell, 1991; Gauthier et al., 1997; Koopman, 2007; Krahn et al., 2004). It is not known whether lipid content is stratified across the blubber of calves, or if stratification is acquired with blubber growth. Also unknown is whether the inner blubber layer is more active and better reflects the nutritional status of calves compared to the outer layer. This is the first study to analyze lipid content of the outer blubber layer in mysticete calves. Although lipid content stratification might probably increase with age in southern right whale calves, we only focused on the outer layer since fat content from dead calf blubber was validated through comparison with superficial biopsy samples from living calves. Biopsy samples cannot be collected from the middle or internal blubber layers due to obvious ethical constraints. Further studies should investigate variation in lipid content of blubber among layers (stratification), body regions (dorsal, lateral, ventral planes along the anterior and posterior regions) and throughout growth in baleen whale calves.

Interestingly, blubber lipid content at the dorsal anterior region decreased with length in dead calves. Furthermore, mean lipid content in samples taken at the dorsal mid-section of living mothers is significantly low compared to that of living calves (C.F.M., unpublished data). Lower lipid contents are associated with reduced insulation in the blubber of whales (Worthy & Edwards, 1990). If growing calves develop thicker layers of blubber around their bodies, which would increase insulation over time, they may equilibrate thermoregulation through decreasing blubber lipid content. By comparison, small body size adult harbor porpoises show higher blubber fat content which probably improves insulation. This is probably advantageous given that the species inhabits cooler coastal waters (Koopman, 2007).

Calves that died in Golfo Nuevo had thicker blubber than those of similar size that died in Golfo San José. In the Valdés calving ground, Golfo Nuevo is where most living whales have been sighted since the 1990s and where most calf deaths have been recorded during high mortality years in the 2000s (Rowntree et al., 2001, 2013; Sironi et al., 2014; Uhart et al., 2008, 2009). Golfo Nuevo may gather females that are both inexperienced (young females with up to three calves recorded) and experienced (older females with more than three calves recorded) that likely give birth to newborns that are small and large in length, respectively (Best & Rüther, 1992; Lockyer, 1990). On the other hand, Golfo San José may assemble mostly inexperienced females since most dead calves recorded there are small. It is possible that calves of inexperienced females have thinner blubber compared to calves of similar sizes that were born from experienced mothers and thus dead calves in Golfo San José were mostly thinner. Current population ecology studies using capture-recapture methods are evaluating whether older females with newborn or neonate calves are sighted more often in Golfo Nuevo than in Golfo San José (M. Agrelo & C.F.M., unpublished data). Other variables such as environmental conditions and social structure may also play a role in whale distribution around the peninsula and require further study.

Overall, we were able to quantitatively characterize progressive increases in blubber thickness in first season calves during growth. Future ontogenic studies should focus on living calves to supplement the findings presented in this study and to incorporate a more complete approach to the study of growth in first-year calves. Ongoing photogrammetric studies are investigating growth rates and changes in body volumes in calves of different ages throughout the calving season at Península Valdés. Current investigations should continue and new avenues for research must be explored to better assess the health of the Península Valdés southern right whale population.

ACKNOWLEDGMENTS

We thank Luciano La Sala, Luciana M. Pozzi, Luciana Musmeci, Nadia Mohamed, Juan Emilio Sala, Julian Andrejuk, Andrea Chirife, Lucas Bandieri, M. Virginia Rago, Silvia Robles, and volunteers of the Southern Right Whale Health Monitoring Program (SRWHMP) for collecting samples from dead calves. Diego Taboada, Roxana Schteinbarg, Luciano Valenzuela, José Carracedo, and volunteers of the Instituto de Conservación de Ballenas (ICB), Fundación Patagonia Natural, and Dr. Denise McAloose, have also provided invaluable support of various kinds. We specially thank Rocío S. Alcalá for helping with lipid content analysis and Ana Fabio Braga for helping with the illustrations. This work was conducted under research permits issued by the Dirección de Fauna y Flora Silvestre and by the Subsecretaría de Turismo y Áreas Protegidas of Chubut Province, Argentina. IACUC approval for collecting biopsy samples from living whales was obtained from the Wildlife Conservation Society’s Institutional Animal Care and Use Committee (protocol #16:02). This work was supported by the Conservation, Research and Education Opportunities International (CREOI) to C.F.M., the American Cetacean Society Grants-in-Aid of Research to C.F.M., Animal Behavior Society - Amy R. Samuels Cetacean Behavior Award to C.F.M., the Global Change & Sustainability Center (GCSC) Research Fund of the University of Utah to C.F.M., the PADI

Foundation grant to C.F.M., the CONICET Postdoctoral Research Fellowship to C.F.M. Funding for the SRHWMP was provided by the Office of Protected Resources of the US National Marine Fisheries Service, National Oceanic and Atmospheric Administration (DG133F-02-SE-0901, DG-133F-06-SE-5823 and DG133F07SE4651), the U.S. Marine Mammal Commission (Grants E4047315 and E4061768), the Ocean Foundation, the Island Foundation, the Pacific Life Foundation, the Lawrence Foundation, FOCA Banco Galicia, the Wildlife Conservation Society, ICB, Ocean Alliance and University of California, Davis.

REFERENCES

Aguilar, A., & Borrell, A. (1990). Patterns of lipid content and stratification in the blubber of fin whales (*Balaenoptera physalus*). *Journal of Mammalogy*, *71*(4), 544–554. https://doi.org/10.2307/1381793

Aguilar, A., & Borrell, A. (1991). Heterogeneous distribution of organochlorine contaminants in the blubber of baleen whales: implications for sampling procedures. *Marine Environmental Research*, *31*(4), 275–286. https://doi.org/10.1016/0141-1136(91)90017-3

Best, P. B., & Rüther, H. (1992). Aerial photogrammetry of southern right whales, *Eubalaena australis*. *Journal of*

Zoology, *228*(4), 595–614. https://doi.org/10.1111/j.1469-7998.1992.tb04458.x

Borrell, A., & Aguilar, A. (1990). Loss of organochlorine compounds in the tissues of a decomposing stranded dolphin. *Bulletin of Environmental Contamination and Toxicology*, *45*, 46–53. https://doi.org/10.1007/BF01701827

Bradford, A. L., Weller, D. W., Ivashchenko, Y. V., Burdin, A. M., & Brownell, R. L., Jr. (2008). *Seasonal and annual variation in body condition of western gray whales off northeastern Sakhalin Island, Russia*. Document SC/60/BRG16 submitted to the International Whaling Commission Scientific Committee.

Bradford, A. L., Weller, D. W., Punt, A. E., Ivashchenko, Y. V., Burdin, A. M., VanBlaricom, G. R., & Brownell, R. L. (2012). Leaner leviathans: body condition variation in a critically endangered whale population. *Journal of Mammalogy*, *93*(1), 251–266. https://doi.org/10.1644/11-MAMM-A-091.1

Brown, M. W., Kraus, S. D., & Gaskin, D. E. (1991). Reaction of North Atlantic right whales (*Eubalaena glacialis*) to skin biopsy sampling for genetic and pollutant analysis. *Report of the International Whaling Commission*, *Special Issue 13*, 81–89.

Brownell, R. J., Jr., & Weller, D. (2001). *Is the "carrying capacity hypothesis" a plausible explanation for the "skinny" gray whale phenomenon?* Document SC/53/BRG20 submitted to the International Whaling Commission Scientific Committee.

Caon, G., Fialho, C. B., & Danilewicz, D. (2007). Body fat condition in franciscanas (*Pontoporia blainvillei*) in Rio Grande do Sul, southern Brazil. *Journal of Mammalogy*, *88*(5), 1335–1341. https://doi.org/10.1644/06-MAMM-A-364R.1

Cawthorn, M. W. (1997). *Meat consumption from stranded whales and marine mammals in New Zealand: Public health and other issues*. Conservation Advisory Science Notes No. 164. Department of Conservation, Wellington, New Zealand. https://www.doc.govt.nz/globalassets/documents/science-and-technical/casn164.pdf

Chirife, A., Uhart, M., Sironi, M., Rago, V., & Rowntree, V. (2014). *Protocolo de necropsia ballena franca austral* (Eubalaena australis) *versión preliminar* [Southern right whale necropsy protocol (*Eubalaena australis*) preliminary version]. Necropsy protocol prepared by Programa Monitoreo Sanitario Ballena Franca Austral [unpublished]. Available from https://www.researchgate.net/publication/336107388

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*(10), e01468. https://doi.org/10.1002/ecs2.1468

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–281. https://doi.org/10.3354/meps12522

Cooke, J. G., Rowntree, V., & Payne, R. (2003). *Analysis of inter-annual variation in reproductive success of South Atlantic right whales* (Eubalaena australis) *from photo-identifications of calving females observed off Península Valdés, Argentina, during 1971-2000*. Document SC/55/023 submitted to the International Whaling Commission Scientific Committee.

Dugail, I., & Guerre-Millo, M. (2009). Overview of the integrative physiology of adipose tissue in energy homeostasis. In G. Frühbeck (Ed.), *Peptides in energy balance and obesity: Frontiers in nutritional science*, (Vol. 4, pp. 331–347). CABI Publishing.

Evans, K., Hindell, M. A., & Thiele, D. (2003). Body fat and condition in sperm whales, *Physeter macrocephalus*, from southern Australian waters. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *134*(4), 847–862. https://doi.org/10.1016/s1095-6433(03)00045-x

Fernández Ajó, A. A., Giese, C., Sironi, M., Uhart, M., Rowntree, V. J., Marón, C. F., Dillon, D., DiMartino, M., & Buck, C. L. (2020). Retrospective analysis of the lifetime endocrine response of southern right whale calves to gull wounding and harassment: A baleen hormone approach. *General and Comparative Endocrinology*, *296*, 113536. https://doi.org/10.1016/j.ygcen.2020.113536

Gauthier, J. M., Metcalfe, C. D, & Sears, R. (1997). Validation of the blubber biopsy technique for monitoring of organochlorine contaminants in balaenopterid whales. *Marine Environmental Research*, *43*(3), 157–179. https://doi.org/10.1016/0141-1136(96)00085-2

Geraci, J. R., & Lounsbury, V. J. (2005). *Marine mammals ashore: A field guide for strandings* (2nd ed.). National Aquarium of Baltimore.

Gulland, F. M. D., & Hall, A. J. (2005). The role of infectious disease in influencing status and trends. In J. E. Reynolds

III, W. F. Perrin, R. R. Reeves , S. Montgomery, & T. J. Ragen (Eds.), *Marine mammal research: Conservation beyond crisis* (pp. 47–62). Johns Hopkins University Press.

Hamilton, J. L., Dillaman, R. M., McLellan, W. A., & Pabst, D. A. (2004). Structural fiber reinforcement of keel blubber in harbor porpoise (*Phocoena phocoena*). *Journal of Morphology*, *261*, 105–117.

International Whaling Commission. (2011). Report of the Southern Right Whale Dieoff Workshop. *Journal of Cetacean Research and Management*, *12* (Suppl.), 367–398.

International Whaling Commission. (2018). *Report of the sub-committee on cetacean stocks that are or might be subject of Conservation Management Plans (CMP)*. Document SC/67B/F09 submitted to the International Whaling Commission Scientific Committee.

Koopman, H. N. (1998). Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *Journal of Mammalogy*, *79*(1), 260–270. https://doi.org/10.2307/1382862

Koopman, H. N. (2007). Phylogenetic, ecological, and ontogenetic factors influencing the biochemical structure of the blubber of odontocetes. *Marine Biology*, *151*, 277–291. https://doi.org/10.1007/s00227-006-0489-8

Koopman, H. N., Pabst, D. A., McLellan, W. A., Dillaman, R.M., & Read, A.J. (2002). Changes in blubber distribution and morphology associated with starvation in the harbor porpoise (*Phocoena phocoena*): evidence for regional differences in blubber structure and function. *Physiological and Biochemical Zoology*, *75*(5), 498–512. https://doi.org/10.1086/342799

Krahn, M. M., Herman, D. P., Ylitalo, G. M., Sloan, C. A., Burrows, D. G., Hobbs, R. C., Mahoney, B., Yanagida, G., Calambokidis, J., & Moore, S. E. (2004). Stratification of lipids, fatty acids and organochlorine contaminants in blubber of white whales and killer whales. *Journal of Cetacean Research and Management*, 6, 175–189.

Kvadsheim, P. H., Folkow, L. P., & Blix, A. S. (1996). Thermal conductivity of minke whale blubber. *Journal of Thermal Biology*, *21*(2), 123–128. https://doi.org/10.1016/0306-4565(95)00034-8

Leaper, R., Cooke, J., Trathan, P., Reid, K., Rowntree, V., & Payne, R. (2006). Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biology Letters*, *2*(2), 289–292. https://doi.org/10.1098/rsbl.2005.0431

Lockyer, C. (1981). Growth and energy budgets of large baleen whales from the Southern Hemisphere. *Mammals in the seas* (Vol. 3, pp. 379–488). F.A.O Fisheries Series.

Lockyer, C. (1987). Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. In A. C. Huntley, D. P. Costa, G. A. J. Worthy, & M. A. Castellini (Eds.), *Approaches to marine mammal energetics* (pp. 183–203). Society of Marine Mammalogy Special Publication Number 1.

Lockyer, C. (1990). The importance of biological parameters in population assessments with special reference to fin whales from the NE Atlantic. In E. Vestergaard (Ed.), *North Atlantic studies: whaling communities* (Vol. 2, pp. 22–31). Aarhus University Press.

Lockyer, C. (1993). Seasonal changes in body fat condition of northeast Atlantic pilot whales, and their biological significance. *Report of the International Whaling Commission*, *Special Issue 14*, 205–234.

Lockyer, C. (1995). Aspects of the morphology, body fat condition and biology of the harbour porpoise, *Phocoena phocoena*, in British waters. *Report of the International Whaling Commission*, *Special Issue 16*, 199–210.

Lockyer, C. (2007). All creatures great and smaller: A study in cetacean life history energetics. *Journal of the Marine Biological Association of the United Kingdom*, *87*(4), 1035–1045. https://doi.org/10.1017/S0025315407054720

Lockyer, C., & Waters, T. (1986). Weights and anatomical measurements of Northeastern Atlantic fin (*Balaenoptera physalus*, Linnaeus) and sei (*B. borealis*, Lesson) whales. *Marine Mammal Science*, *2*(3), 169–185. https://doi.org/10.1111/j.1748-7692.1986.tb00039.x

Lockyer, C. H., McConnell, L. C., & Waters, T. D. (1984). The biochemical composition of fin whale blubber. *Canadian Journal of Zoology*, *62*(12), 2553–2562. https://doi.org/10.1139/z84-373

Lockyer, C. H., McConnell, L. C., & Waters, T. D. (1985). Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. *Canadian Journal of Zoology*, *63*, 2328–2338. https://doi.org/10.1139/z85-345

Marón, C. F., Beltramino, L., Di Martino, M., Chirife, A., Seger, J., Uhart, M., Sironi, M., & Rowntree V. J. (2015). Increased wounding of southern right whale (*Eubalaena australis*) calves by Kelp Gulls (*Larus dominicanus*) at

Península Valdés, Argentina. *PLoS ONE*, *10*(10), e0139291. https://doi.org/10.1371/journal.pone.0139291

Marón C. F., Budge S. M., Ward R. E., Valenzuela L. O, Di Martino M., Ricciardi, M., Sironi1, M., Uhart, M., Seger, J., & Rowntree V. J. (2020). Evaluation of fatty acids and stable isotope ratios in southern right whale calves (*Eubalaena australis*) in relation to age and mortality at Península Valdés, Argentina. *Marine Ecology Progress Series*, *646*, 189–200. https://doi.org/10.3354/meps13387

Marón, C. F., Rowntree, V. J., Sironi, M., Uhart, M., Payne, R. S., Adler F. R., Seger J. (2015). *Estimating population consequences of increased calf mortality in the southern right whales off Argentina*. Document SC/66a/BRG/1 submitted to the International Whaling Commission Scientific Committee.

McAloose, D., Rago, M. V., Di Martino, M., Chirife, A., Olson, S. H., Beltramino, L., Pozzi, L. M., Musmeci, M., La Sala, L., Mohamed, N., Sala, J. E., Bandieri, L., Andrejuk, J., Tomaszewicz, A., Seimon, T., Sironi, M., Samartino, L. E., Rowntree, V., & Uhart, M. (2016). Post-mortem findings in southern right whales *Eubalaena australis* at Península Valdés, Argentina, 2003-2012. *Diseases of Aquatic Organisms*, *119*, 17–36. https://doi.org/10.3354/dao02986

Miller, C. A., Best, P. B., Perryman ,W. L., Baumgartner, M. F., & Moore, M. J. (2012). Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. *Marine Ecology Progress Series*, *459*, 135–156. https://doi.org/10.3354/meps09675

Miller, C. A., Reeb, D., Best, P. B., Knowlton, A. R., Brown, M. W., & Moore, M. J. (2011). Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. *Marine Ecology Progress Series*, *438*, 267–283. https://doi.org/10.3354/meps09174

Moore, M. J., Knowlton, A. R, Kraus, S. D., McLellan, W. A., & Bonde, R. K. (2004). Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970–2002). *Journal of Cetacean Research and Management*, *6*, 199–214.

Moore, S. E., Urbán, J. R., Perryman, W. L., Gulland, F., Perez-Cortes, H. M., Wade P. R., Rojas-Bracho, L., & Rowles T. (2001). Are gray whales hitting “K” hard? *Marine Mammal Science, 17*(4), 954–958. https://doi.org/10.1111/j.1748-7692.2001.tb01310.x

Næss, A., Haug, T., & Nilssen, E. M. (1998). Seasonal variation in body condition and muscular lipid contents in Northeast Atlantic minke whale, *Balaenoptera acutorostrata*. *Sarsia*, *83*(3), 211–218. https://doi.org/10.1080/00364827.1998.10413682

Noren, S. R., & Wells, R. S. (2009). Blubber deposition during ontogeny in free-ranging Bottlenose Dolphins: Balancing disparate roles of insulation and locomotion. *Journal of Mammalogy*, *90*(3), 629–637.

Nousek-McGregor, A. E., Miller, C. A., Moore, M. J., & Nowacek, D. P. (2014). Effects of body condition on buoyancy in endangered North Atlantic right whales. *Physiological and Biochemical Zoology*, *87*(1), 160–171. https://doi.org/10.1086/671811

Pabst, D. A., Hamilton, J. L, McLellan, W. A., Williams, T. M., & Gosline, J. L. (1999). Streamlining dolphins: designing soft-tissue keels. *Proceedings of the 11th International Symposium on Unmanned Untethered Submersible Technology* (pp. 477–486). University of New Hampshire-Marine Systems.

Parry, D. A. (1949). The structure of whale blubber, and a discussion of its thermal properties. *Quarterly Journal of Microscopical Science*, *3*, 13–25.

Pettis, H. M., Rolland, R. M., Hamilton, P. K., Brault, S., Knowlton, A. R., & Kraus, S. D. (2004). Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. *Canadian Journal of Zoology*, *82*(1), 8–19. https://doi.org/10.1139/z03-207

Pond, C. M. (1978). Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annual Review of Ecology Evolution and Systematics*, *9*, 519–570. https://doi.org/10.1146/annurev.es.09.110178.002511

R Core Team (2019). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing.

Reeb, D., Best, P. B., & Kidson, S. H. (2007). Structure of the integument of southern right whales, *Eubalaena australis*. *The Anatomical Record*, *290*(6), 596–613. https://doi.org/10.1002/ar.20535

Rowntree, V. J., Payne, R. S., & Schell, D. M. (2001). Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. *Journal of Cetacean Research and Management*, *2*, 133–143. https://doi.org/10.47536/jcrm.vi.298

Rowntree, V. J., Uhart, M., Sironi, M., Chirife, A., Di Martino, M., La Sala, L., Musmeci1, L., Mohamed, N., Andrejuk, J., McAloose, D., Sala1, J. E., Carribero, A., Rally, H., Franco, M., Adler, F. R., Brownell, R. L., Jr., Seger, J., & Rowles T. (2013). Unexplained recurring high mortality of southern right whale *Eubalaena australis* calves at Península Valdés, Argentina. *Marine Ecology Progress Series*, *493*, 275–289. https://doi.org/10.3354/meps10506

Ryan, C., McHugh, B., Boyle, B., McGovern, E., Bérubé, M., Lopez-Suárez, P., Elfes, C. T., Boyd, D. T., Ylitalo, G. M., Van Blaricom, G. R., Clapham, F. J., Robbins, J., Palsbøll, P. J., O'Connor, I., & Berrow, S. D. (2013). Levels of persistent organic pollutants in eastern North Atlantic humpback whales. *Endangered Species Research*, *22*, 213–223. https://doi.org/10.3354/esr00545

Ryg, M., Smith, T. G., & Øritsland, N. A. (1988). Thermal significance of the topographical distribution of blubber in ringed seals (*Phoca hispida*). *Canadian Journal of Fisheries and Aquatic Sciences*, *45*(6), 985–992. https://doi.org/10.1139/f88-121

Sironi, M., Rowntree, V., Di Martino, M., Alzugaray, L., Rago, V., Marón, C. F., & Uhart, M. (2018). *Southern right whale mortalities at Península Valdés, Argentina: updated* *information for 2016-2017*. Document SC/67B/CMP/06 submitted to the International Whaling Commission Scientific Committee.

Sironi, M., Rowntree, V. J., Di Martino, M., Beltramino, L., Rago, V., Marón, C. F., & Uhart, M. (2014). *Updated information for 2012-2013 on southern right whale mortalities at Península Valdés, Argentina*. Document SC/65b/BRG06 submitted to the International Whaling Commission Scientific Committee.

Sironi, M., Rowntree, V. J., Di Martino, M., Beltramino, L., Rago, V., Marón, C. F., & Uhart, M. (2016). *Southern right whale mortalities at Península Valdés, Argentina: updated information for 2014-2015*. Document SC/66b/BRG/02 submitted to the International Whaling Commission Scientific Committee.

Slijper, E. J. (1948). On the thickness of the layer of blubber in Antarctic blue and fin whales. *1st Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, *51*, 1033–1316.

Struntz, D., McLellan, W. A., Dillaman, R. M., Blum, J. E., Kucklick, J. R., & Pabst, D. A. (2004). Blubber development in bottlenose dolphins (*Tursiops truncatus*). *Journal of*

Morphology, *259*(1), 7–20. https://doi.org/10.1002/jmor.10154

Summers, A. (2001). Spring-loaded. Every beat of a dolphin’s tail stores elastic energy that helps propel the animal forward. *Natural History*, *110*, 76–77.

Thomas, P. O., & Taber, S. M. (1984). Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behaviour*, *88*(1–2), 42–60. https://doi.org/10.1163/156853984X00470

Thomas, P. O., Uhart, M., McAloose, D., Sironi, M, Rowntree, V. J., Brownell, R. L., Jr., Gulland, F. M. D., Moore, M. M., Marón, C., & Wilson, C. (2013). *Workshop on the Southern right whale die-off at Península Valdés, Argentina*. Document SC/65a/BRG15 submitted to the International Whaling Commission Scientific Committee.

Toedt, M. E. (2001). *A histological and ultrastructural examination of the integument of* Delphinus delphis [Master’s thesis]. University of North Carolina, Wilmington.

Tormosov, D. D., Mikhaliev, Y. A., Best, P. B., Zemsky, V. A., Sekiguchi, K., & Brownell, R. L., Jr. (1998). Soviet catches of southern right whales *Eubalaena australis*, 1951–1971. Biological data and conservation implications.

Biological Conservation, *86*(2), 185–197. https://doi.org/10.1016/S0006-3207(98)00008-1

Uhart, M., Rowntree, V. J., Mohamed, N., Pozzi, L., La Sala, L., Andrejuk, J., Musmeci, L., Franco, M., Sironi, M., Sala, J. E., McAloose, D., Moore, M., Tohuey, K., McLellan, W. A., & Rowles, T. (2008). *Strandings of southern right whales* (Eubalaena australis) *at Península Valdés, Argentina from 2003-2007*. Document SC/60/BRG15 submitted to the International Whaling Commission Scientific Committee.

Uhart, M., Rowntree, V. J., Sironi, M., Chirife, A., Mohamed, N., Pozzi, L., Musmeci, L., Franco, M., McAloose, D., Doucette, G., Sastre, V., & Rowles, T. (2009). *Continuing southern right whale mortality events at Península Valdés, Argentina*. Document SC/61/BRG18 submitted to the International Whaling Commission Scientific Committee.

Whitehead, H., & Payne, R. (1981). New techniques for assessing populations of right whales without killing them. *Mammals in the seas* (Vol. 3, pp. 189–208). F.A.O Fisheries Series.

Worthy, G. A. J, & Edwards, E. F. (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*). *Physiological Zoology*, *63*(2), 432–442. https://doi.org/10.1086/physzool.63.2.30158506

Zerbini, A. N., Rosenbaum, H., Mendez, M., Sucunza, F., Andriolo, A., Harris, G., Clapham, M., Sironi, M., Uhart. A., & Fernandez-Ajó, A. (2016). *Tracking southern right whales through the southwest Atlantic: An update on movements, migratory routes and feeding grounds*. Document SC/66b/BRG26 submitted to the International Whaling Commission Scientific Committee.

TABLE 1 Mean and standard deviation of blubber thickness measurements in different calf age classes for all stranding years (2003–2019) and in high (2003, 2005, 2007–2013) and low (2004, 2006, 2014–2019) mortality years. Age classes include newborn and neonate (<5 m), young calf (5–7 m), and old calf (7–9 m) (McAloose et al., 2016). Blubber thickness was measured following the cranio-caudal axis at the dorsal, lateral, and ventral sites along the axillary (1), umbilical (2), and anal (3) girths. Blubber measurements are expressed in centimeters and length measurements in meters. Data were collected during 350 necropsies from 2003 to 2019 at Península Valdés, Argentina.

Age class	**Blubber measuring site**	**All years**	**Low mortality year**	**High mortality year**	**% increase compared to previous age**
Newborn and neonate	Dorsal-1	2.96 ± 1.31 (*n* = 65)	2.76 ± 1.01 (*n* = 18)	3.03 ± 1.41 (*n* = 47)	—
(<5 m)	Dorsal-2	3.71 ± 1.35 (*n* = 63)	3.52 ± 0.98 (*n* = 18)	3.79 ± 1.47 (*n* = 45)	—
	Dorsal-3	5.21 ± 1.96 (*n* = 63)	5.19 ± 1.45 (*n* = 18)	5.21 ± 2.14 (*n* = 45)	—
	Lateral-1	4.10 ± 1.47 (*n* = 78)	3.86 ± 1.03 (*n* = 25)	4.02 ± 1.63 (*n* = 53)	—

	Lateral-2	4.11 ± 1.37 (*n* = 78)	3.89 ± 1.02 (*n* = 25)	4.23 ± 1.50 (*n* = 53)	—
	Lateral-3	4.64 ± 1.48 (*n* = 74)	4.72 ± 1.21 (*n* = 25)	4.6 ± 1.61 (*n* = 49)	—
	Ventral-1	4.41 ± 1.14 (*n* = 46)	4.28 ± 0.85 (*n* = 15)	4.46 ± 1.26 (*n* = 31)	—
	Ventral-2	4.37 ± 1.36 (*n* = 45)	3.97 ± 0.87 (*n* = 14)	4.65 ± 1.49 (*n* = 31)	—
	Ventral-3	6.40 ± 1.60 (*n* = 41)	6.38 ± 1.12 (*n* = 13)	6.41 ± 1.80 (*n* = 28)	—
Young calf (5-7 m)	Dorsal-1	4.30 ± 1.62 (*n* = 149)	4.07 ± 1.65 (*n* = 27)	4.35 ± 1.61 (*n* = 122)	45.27
	Dorsal-2	5.23 ± 1.93 (*n* = 149)	4.81 ± 1.82 (*n* = 26)	5.32 ± 1.95 (*n* = 123)	40.97
	Dorsal-3	7.28 ± 2.69 (*n* = 149)	6.38 ± 2.28 (*n* = 26)	7.48 ± 2.74 (*n* = 123)	39.73
	Lateral-1	6.29 ± 2.55 (*n* = 198)	5.11 ± 1.83 (*n* = 38)	6.57 ± 2.63 (*n* = 160)	53.41
	Lateral-2	6.52 ± 2.31 (*n* = 197)	5.84 ± 2.29 (*n* = 37)	6.68 ± 2.29 (*n* = 160)	58.64
	Lateral-3	6.63 ± 2.05 (*n* = 188)	6.29 ± 1.66 (*n* = 36)	6.71 ± 2.13 (*n* = 152)	42.89
	Ventral-1	6.39 ± 2.16 (*n* = 113)	5.95 ± 2.21 (*n* = 19)	6.48 ± 2.15 (*n* = 94)	44.9
	Ventral-2	6.74 ± 2.43 (*n* = 121)	6.59 ± 2.49 (*n* = 18)	6.78 ± 2.43 (*n* = 103)	54.23
	Ventral-3	8.39 ± 2.64 (*n* = 118)	8.53 ± 3.08 (*n* = 18)	8.36 ± 2.57 (*n* = 100)	31.09

Old calf (7–9 m)	Dorsal-1	8.62 ± 2.01 (*n* = 25)	8.25 ± 0.35 (*n* = 2)	8.66 ± 2.09 (*n* = 23)	100.47
	Dorsal-2	9.99 ± 2.93 (*n* = 25)	9.5 ± 2.12 (*n* = 2)	10.03 ± 3.03 (*n* = 23)	91.01
	Dorsal-3	12.37 ± 3.24 (*n* = 23)	12.25 ± 2.47 (*n* = 2)	12.39 ± 3.36 (*n* = 21)	69.09
	Lateral-1	10.82 ± 2.88 (*n* = 38)	12.33 ± 2.51 (*n* = 3)	10.69 ± 2.91 (*n* = 35)	72.02
	Lateral-2	11.20 ± 2.54 (*n* = 40)	11.17 ± 0.29 (*n* = 3)	11.21 ± 2.64 (*n* = 37)	71.78
	Lateral-3	10.44 ± 2.93 (*n* = 37)	11.5 ± 1.8 (*n* = 3)	10.34 ± 3.01 (*n* = 34)	57.47
	Ventral-1	10.54 ± 2.37 (*n* = 21)	11.8 (*n* = 1)	10.47 ± 2.41 (*n* = 20)	64.95
	Ventral-2	11.71 ± 2.59 (*n* = 26)	10.1 (*n* = 1)	11.78 ± 2.63 (*n* = 25)	73.74
	Ventral-3	12.38 ± 2.57 (*n* = 24)	11.8 (*n* = 1)	12.41 ± 2.81 (*n* = 23)	47.56

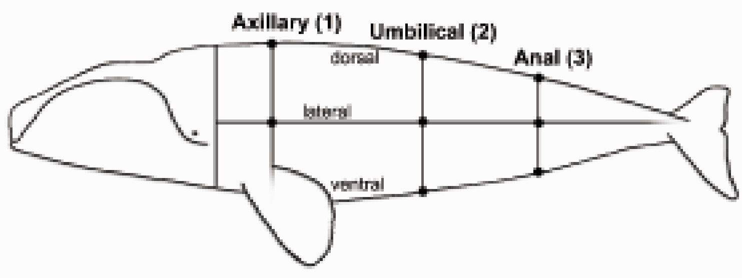
FIGURE 1 Measuring sites on the body of southern right whales. Blubber thickness was measured following the cranio-caudal axis at the dorsal, lateral, and ventral sites along the axillary (1), umbilical (2), and anal (3) girths. (The ventral-axillary measurement is behind the pectoral fin and not shown in the drawing).

FIGURE 2 Blubber thickness measurements along nine different body sites in calves of all ages. Blubber thickness was measured following the cranio-caudal axis at the dorsal, lateral, and ventral sites along the axillary (1), umbilical (2), and anal (3) girths. Blubber thickness is expressed in centimeters. Open circles indicate outliers and correspond to measurements taken from old calves (from 7 to 8.4 m long). Data were collected during necropsies from 2003 to 2019 at Península Valdés, Argentina. Abbreviations: dorsal-1 (dorsal-axillary), dorsal-2 (dorsal-umbilical), dorsal-3 (dorsal-anal), lateral-1 (lateral-axillary), lateral-2 (lateral-umbilical), lateral-3 (lateral-anal), ventral-1 (ventral-axillary), ventral-2 (ventral-umbilical), ventral-3 (ventral-anal).

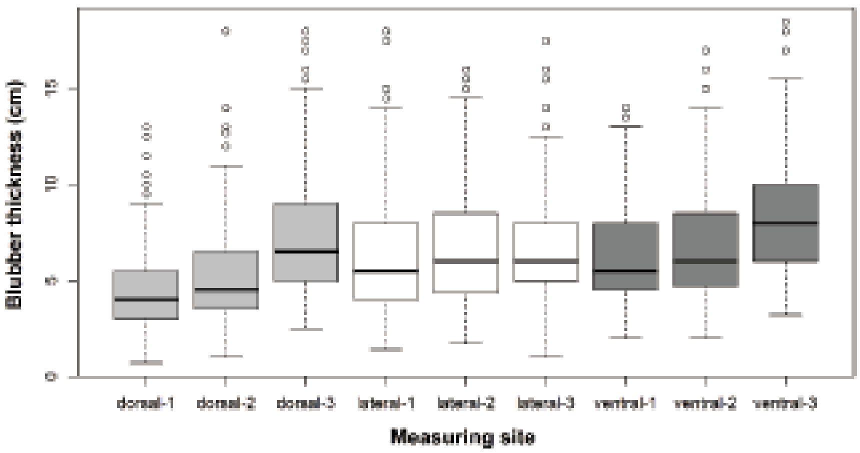
FIGURE 3 Blubber thickness measurements (n = 2,206) in 350 dead calves in different states of decay and adjusted by length. Blubber thickness is expressed in centimeters and length in meters. Blubber thickness presented in this figure was measured at dorsal, lateral, and ventral sites along the axillary, umbilical, and anal girths (maximum of nine measurements per stranded calf). Carcasses in condition code 2 were fresh (orange dots and line); in condition code 3, calves presented a white-yellowish blubber with mild odor (brown dots and line), and in condition code 4, blubber had a strong odor, but was still soft and maintained structure and whitish coloration (blue dots and line). Notice that blubber thickness measurements overlap in calves from 4.5 to 6 m long for all condition codes (2, 3, and 4).

FIGURE 4 Changes in dorsal, ventral, and lateral blubber with calf length. Blubber thickness was measured in centimeters and length in meters. Along the cranio-caudal axis, blubber increased dorsally and ventrally. Laterally, blubber was thinner at the lateral-3 site (close to the peduncle), favoring streamlining. Whale silhouettes show how blubber (in light pink) thickens along the dorsal, lateral, and ventral planes of the body. Abbreviations: dorsal-1 (dorsal-axillary), dorsal-2 (dorsal-umbilical), dorsal-3 (dorsal-anal), lateral-1 (lateral-axillary), lateral-2 (lateral-umbilical), lateral-3 (lateral-anal), ventral-1 (ventral-axillary), ventral-2 (ventral-umbilical), ventral-3 (ventral-anal).

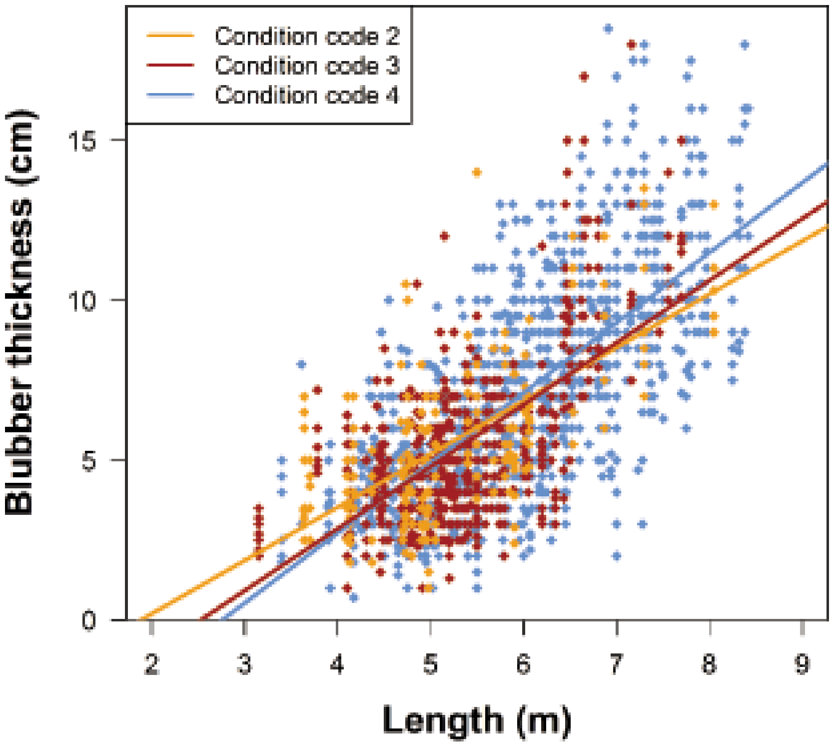
FIGURE 5 Changes in axillary, umbilical, and anal blubber with calf length. Blubber thickness was measured in centimeters and length in meters. On the axillary and umbilical girths, blubber thickness was lower in the dorsal surface compared to the ventral and lateral sites. On the anal girth (closer to the peduncle), blubber was thinner at the lateral-3 site than at the upper dorsal and lower ventral sites. Transversal cuts show how blubber (in light pink) thickens throughout the axillary, umbilical, and anal girths. Abbreviations: dorsal-1 (dorsal-axillary), lateral-1 (lateral-axillary), ventral-1 (ventral-axillary), dorsal-2 (dorsal-umbilical), lateral-2 (lateral-umbilical), ventral-2 (ventral-umbilical), dorsal-3 (dorsal-anal), lateral-3 (lateral-anal), ventral-3 (ventral-anal).



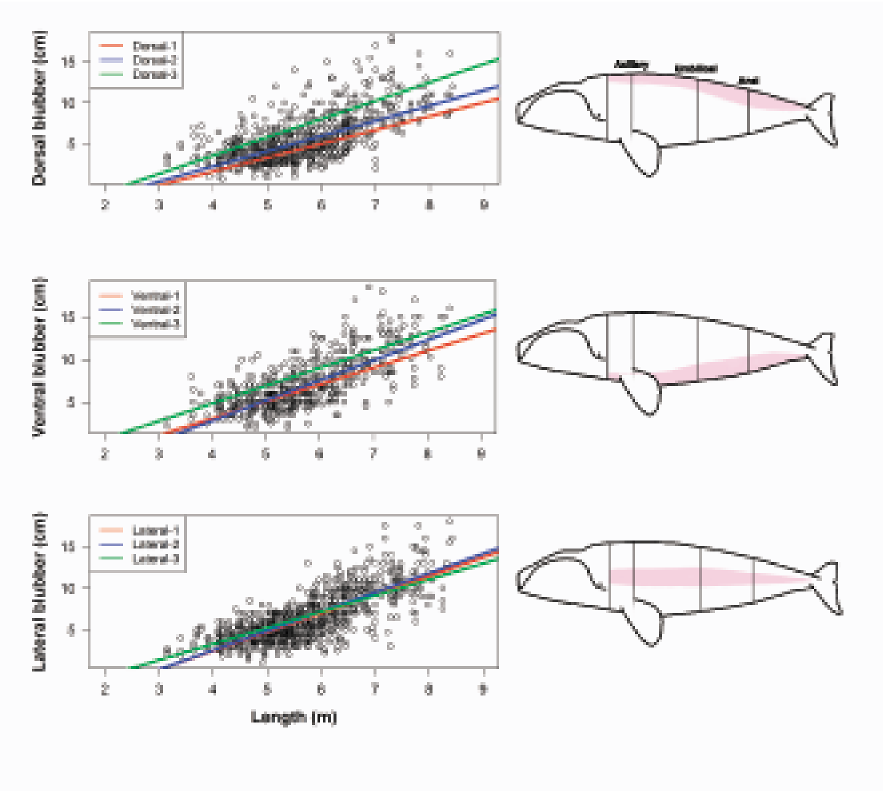
MMS_12818_5005_Fig 1 copy.tif



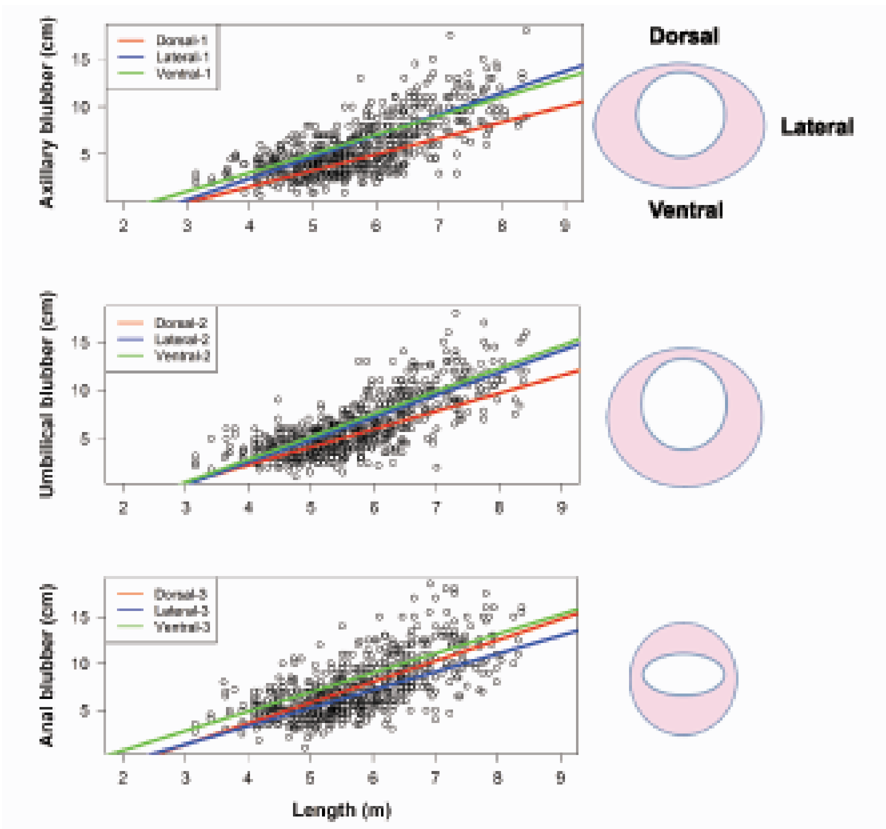
MMS_12818_5005_Fig 2 copy.tif



MMS_12818_5005_Fig 3 copy.tif



MMS_12818_5005_Fig 4 copy.tif



MMS_12818_5005_Fig 5 copy.tif

TABLE S1 Individual variables for the dead calves included in blubber thickness comparisons. Year of sample collection is presented and further categorized as low and high calf mortality years. High mortality years are highlighted in yellow. The number of blubber thickness measurements includes the sum of the measurements taken at all body sites (dorsal-1, -2, -3; lateral -1, -2, -3; and ventral-1, -2, -3). Calf length is provided in meters. Age classes include newborn or neonate (Neo) (< 5 m), young calf (Yo) (5–7 m), or old calf (7–9 m) (McAloose et al., 2016). Abbreviations: Sex: female (F) or male (M); Necropsy condition: fresh (Fr), moderate (Mo) or advanced (Ad) decomposition (Geraci & Lounsbury 2005); Area: Golfo Nuevo (GN) or Golfo San José (GSJ). U: Unknown.

Year	**Low or High mortality**	**No. of dead calves used for this analysis (% of that year's total calf deaths)**	**No. of blubber thickness measurements**	**Length range (m)**	**% Age classes (Neo/Yo/Old)**	**% Sex (F/M/U**	**% Necropsy condition (Fr/Mo/ Ad/U)**	**% Area (GN/GSJ)**
2003	High	14 (48%)	94	3.8–6.8	43/57/0	43/54/08	14/29/57/0	57/43
2004	Low	5 (38%)	39	4.6–6.7	60/40/0	40/60/0	20/40/40/0	80/20
2005	High	5 (14%)	26	4.9–6.9	40/60/0	80/20/0	40/20/40/0	60/40
2006	Low	6 (38%)	36	4.8–7.7	17/66/17	83/17/0	17/33/50/0	50/50
2007	High	4 (5%)	22	6.8–8.4	0/25/75	25/50/25	25/50/25/0	75/25
2008	High	28 (31%)	52	4.7 – 7.5	18/64/18	43/52/12	7/21/64/7	57/43
2009	High	55 (75%)	363	3.4–8.4	18/73/9	51/47/4	13/9/73/5	85/15
2010	High	37 (93%)	261	4.1–7.9	22/56/22	43/57/0	19/16/65/0	65/35
2011	High	43 (74%)	291	3.6–8.3	33/47/20	51/49/0	7/40/53/0	81/19
2012	High	72 (64%)	485	3.1–8.3	18/74/8	44/50/6	7/21/72/0	86/14
2013	High	24 (38%)	165	4.3–7.6	13/66/21	50/42/8	0/38/62/0	92/8
2014	Low	10 (50%)	69	4.4–7	20/70/10	60/40/0	10/40/50/0	70/30
2015	Low	22 (58%)	152	4.2–7.4	50/45/5	59/36/5	0/36/64/0	68/32
2016	Low	11 (79%)	69	3.9–6.5	55/45/0	55/36/9	0/64/36/0	82/18
2017	Low	7 (26%)	37	4.5–6.6	29/71/0	71/29/0	0/57/43/0	86/14
2018	Low	5 (23%)	32	4.5 – 6.5	20/80/0	40/60/0	0/40/60/0	60/40
2019	Low	2 (20%)	13	5.6–6.5	0/100/0	0/1/1	0/100/0/0	100/0
17 years	**8** Low **9** High	**350** calves	**2,206** measurements	**3.1–8.4** m long	**25%** neonates and newborns **62%** young calves **13%** old calves	**49%** female **46%** male	**9%** fresh **27%** moderate **62%** advanced	**77%** GN **23%** GSJ

TABLE S2 Individual variables for lipid content analysis in the blubber of dead calves. Lipid content was analyzed in samples from low and high calf mortality years. High mortality years are highlighted in yellow. Samples were taken mainly from the dorsal anterior region of the calf's body (81%). Calf length is provided in meters. Age classes include: newborn or neonate (Neo) (<5 m), young calf (Yo) (5–7 m), or old calf (7–9 m) (McAloose et al., 2016). Abbreviations: Sex: female (F) or male (M); Necropsy condition: fresh (Fr) or moderate (Mo) decomposition (Geraci & Lounsbury, 2005); Area: Golfo Nuevo (GN) or Golfo San José (GSJ). U: Unknown.

Year	**Low or High mortality**	**No. of dead calves used for this analysis (% of that year's total calf deaths)**	**No. of blubber samples for lipid analysis**	**Length range (m)**	**% Age classes (Neo/Yo/Old)**	**% Sex (F/M/U)**	**% Necropsy condition (Fr/Mo)**	**% Area (GN/GSJ)**
2009	High	2 (3)	2	4.50–5.85	50/50/0	100/0/0	50/50	0/100
2010	High	12 (30)	12	4.10–7.30	58/34/8	50/50/0	58/42	75/25
2011	High	13 (22)	13	3.64–6.45	46/54/0	38/62/0	15/85	77/23
2012	High	15 (13)	15	3.70–6.87	33/67/0	60/40/0	33/67	80/20
2014	Low	4 (20)	4	4.37–6.20	25/75/0	25/75/0	25/75	100/0
2015	Low	8 (21)	8	4.31–5.89	50/50/0	100/0/0	0/100	75/25
2016	Low	5 (36)	5	4.78–6.50	40/60/0	40/40/20	0/100	80/20
7 years	**3** Low **4** High	**59** calves	**59** samples	3.64–7.30	**44%** neonates and newborns **54%**young calves **2%** old calves	**56%** female **42%** male	**27%** fresh **73%** moderate	**76%** GN **24%** GSJ

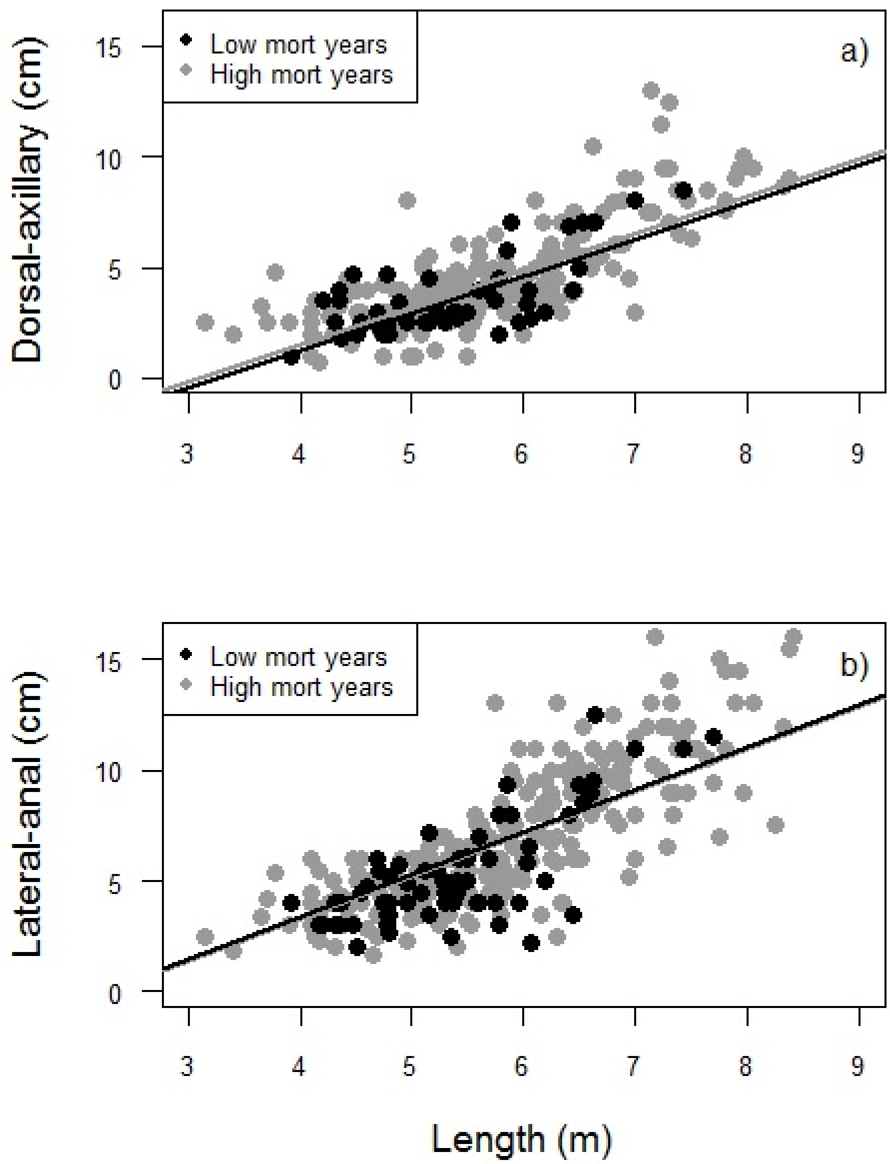


FIGURE S1 Blubber thickness in relation to length for calves that stranded in low mortality (black dots) and high mortality (gray dots) years. Blubber thickness was measured in centimeters and length in meters. (a) and (b) illustrate two out of nine blubber measurement locations, the dorsal-axillary and the lateral-anal positions. Data were collected during necropsies from 2003 to 2019 at Península Valdés, Argentina.