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INTERNATIONAL WHALING COMMISSION

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ABSTRACT

Marine mammals rely on their subcutaneous fat layer or blubber to store energy, insulate their bodies and provide buoyancy and streamlining. Right whale calves are born with a thin blubber layer and need maternal milk to increase lipid reserves and grow. From 2003 to 2017, at least 706 southern right whale (*Eubalaena australis*) calves died at Península Valdés (Argentina) calving ground. Malnutrition has been considered as possible contributor to these deaths because it may negatively affect body condition of calves. However, anatomical signs of starvation were not evident during necropsies of calf carcasses. We measured blubber thickness in nine body locations of 345 dead calves to determine whether their blubber was thinner in years with high calf mortality (2003, 2005, 2007-2013) compared to low mortality years (2004, 2006, 2014-2017). Additionally, we asked whether blubber thickness changed with calf length, sex, state of decay and stranding location along the dorsal, lateral and ventral planes of the body. We also analyzed whether the lipid content of the external blubber layer varies among living (n=16) and dead (n=67) calves of similar lengths. Contrary to what we expected, when controlled for calf length and state of decay, our data suggest that blubber was not significantly thinner in high mortality years compared to low mortality years and its lipid content did not vary significantly among living and dead calves. The only variable we found to affect blubber thickness was calf length as it increased as calves grew at all body locations. These findings do not suggest a decline in the blubber condition of calves over the period examined. Moreover, they do not support the hypothesis of reduced transfer of maternal fat reserves to calves in high mortality years. However, this hypothesis should not be discarded, and additional studies should be conducted to further assess the overall health and body condition of right whale calves at Península Valdés.

INTRODUCTION

Adipose tissue is an important energy reservoir in mammals (Pond 1978, Dugail & Guerre-Millo 2009). Blubber, a subcutaneous layer composed of fat cells and collagen, is the most important store of fat reserves in marine mammals and also provides insulation, buoyancy and streamlining (Parry 1949, Lockyer 1984, Kvadsheim et al. 1996, Toedt 2001, Struntz & McLellan 2004, Rosen et al. 2007). Blubber allows marine mammals such as baleen whales to alternate between feeding and fasting by sustaining self-maintenance, migration and reproduction (Lockyer 1986, 1987, Oftedal 1993, 2000). From 2003 to 2017, at least 706 southern right whale (*Eubalaena australis*) calves died on the Península Valdés calving ground from some as yet unidentified cause(s) (Uhart et al. 2009, International Whaling Commission [IWC] 2011, Thomas et al. 2013, Rowntree et al. 2013, Sironi et al. 2016). Poor nutritional state of mothers has been proposed as a potential contributor to these calf deaths (IWC 2011, Thomas et al. 2013).

Blubber thickness can be used as an indicator of body fat condition in dead and living cetaceans since it is known to change with the nutritional and reproductive status of individuals (Lockyer 1986, 2007, Koopman et al. 2002, Gulland & Hall 2005, Miller et al. 2011, 2012, Bradford et al. 2012). For example, ultrasound measurements of blubber thickness of living North Atlantic (*E. glacialis*) and southern right whale calves off South Africa indicate that their body fat condition improves during the first months of life on their calving grounds but decreases after weaning in *E. glacialis* (Miller et al. 2011, 2012). We compared blubber thickness in different body locations of calves that died from 2003 to 2017 to evaluate whether their blubber thickness varied between years with low and high calf mortality. We also determined whether blubber thickness was affected by sex or stranding locations at Península Valdés (Golfo Nuevo vs. Golfo San José), Argentina.

In addition to blubber thickness, reductions in lipid content can also be indicative of changes in the body condition of cetaceans and signal food deprivation or starvation as has been documented in gray whales *Eschrichtius robustus* (Gulland et al. 2005). These authors found a significant reduction of lipid content in the blubber of stranded whales that were presumed to have died from food deprivation when compared to individuals harvested by whalers. We compared lipid content in blubber of dead and living southern right whale calves to evaluate whether dead calves showed depleted fat reserves that were independent of their state of decomposition.

MATERIALS AND METHODS

Data collection from dead calves

Forensic examinations of dead southern right whale calves were conducted at Península Valdés (Golfo Nuevo and Golfo San José, Fig. 1) by the Southern Right Whale Health Monitoring Program (SRWHMP) from June to December in 2003-2017. The SRWHMP team recorded blubber thickness, total length, carcass decomposition and sex of individuals, along with date of necropsy and stranding location. The necropsied calves ranged in age from newborns to around four months of age (Uhart et al. 2008, 2009, Sironi et al. 2014, McAloose et al. 2016, Sironi et al. 2016). The majority of calves died during the high calf mortality years of 2003, 2005 and 2007-2013 when deaths were significantly greater than expected. Fewer calves died in the low mortality years (2004, 2006, 2014-2017) when the number of dead calves was not significantly greater than expected based on the population's long-term growth rate (Rowntree et al. 2013, Marón et al. 2015a).

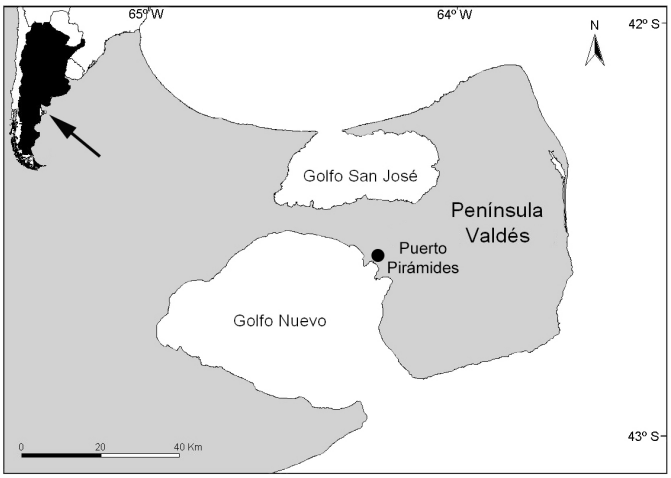

Figure 1. Location of Golfo San José and Golfo Nuevo at Península Valdés, Argentina.

Blubber thickness measurements

Blubber thickness of dead calves was determined *in situ* in calves that died at three body girths when allowed by their stranding 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, Fig. 2). A longitudinal cranial-caudal cut was made first, followed by

three lateral cuts at the axillary (measured at the posterior insertion of the flipper), umbilical and anal girths. After each lateral cut, blubber thickness was measured at the dorsal, lateral and ventral sites. Dorsal or ventral blubber thickness was not determined in whales 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. Blubber thickness was measured 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). Measuring blubber thickness in areas of the back affected by gull lesions was avoided since the wounds can extend from the skin to the blubber layer, thus affecting measurements.

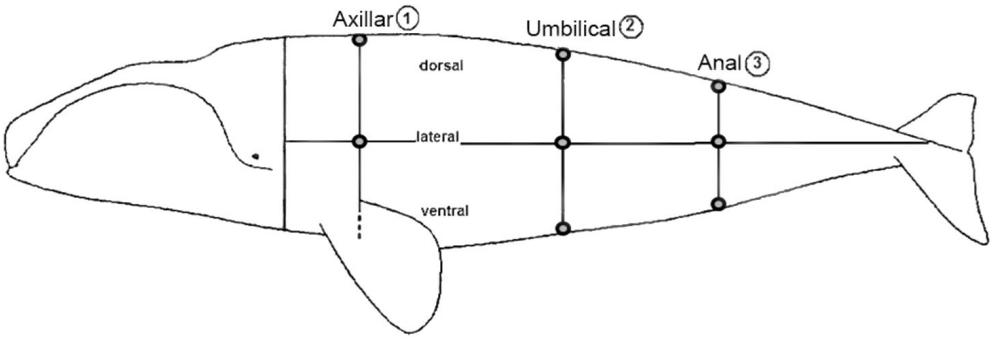

Figure 2. Measuring sites on the body of southern right whales. Blubber thickness was measured following the cranio-caudal axis at the dorsal, lateral and ventral sites along the axillary (-1), umbilical (-2) and anal (-3) girths. (The ventral-axillary measurement is not shown in the drawing).

Length measurements
Dead calf length was used as a proxy for age. In this study, all blubber thickness comparisons were adjusted for calf length because blubber thickness increases with calf age, as shown in living southern right whales off South Africa (Miller et al. 2012). Total length was measured with a measuring tape in a straight line from snout-tip to fluke notch (not following the curve of the body) independently of the whale's stranding position.

Carcass decomposition
A necropsy carcass condition code was assigned to each calf based on the state of decomposition of tissues and organs (Uhart et al. 2009). For this study, only dead calves in conditions 2 (freshly dead), 3 and 4 (Geraci &Lounsbury 2005) were selected and all blubber thickness comparisons were adjusted for necropsy carcass condition (see Statistical Analyses).

Blubber samples from dead calves for lipid content analysis
Blubber samples were collected only from calves that died in 2009-2016 and only from calves that were > 6 m to enable comparison with living calves (see section below). Samples were used if they came from whales in condition code 2 (fresh) and condition code 3 (moderate decomposition) (Geraci & Lounsbury 2005). A full blubber sample with skin attached was removed from each whale at different body locations but primarily along the dorsal plane of the body (65%) to make them comparable to blubber biopsy samples collected from living calves. Blubber samples ranged in size from 5x5 to 15x15 cm and were stored frozen at -20C and/or at -80C in airtight plastic bags until analysis. A horizontal blubber core (0.8 cm in diameter × 4 cm long) was drilled from the outer blubber layer of each frozen sample at 1 cm below the beginning of the dermal layer to resemble blubber biopsies from living whales (which include only the outer blubber layer). We removed the extremes of the core (which were in contact with the air and thus more prone to oxidation) and used the middle section for lipid content analysis.

Blubber samples from living calves for lipid content analysis
Biopsy samples of skin and blubber from living calves were collected in 2016 at Golfo San José, Península Valdés, using darts propelled by a crossbow (Brown et al. 1991). Samples were taken dorsally, mainly from the midsection of the body. Small calves (shorter than 6 m) were not biopsied, hence all living calves that were biopsied were considered to be large (> 6 m). The biopsy darts were fitted with tips 0.5 cm in

diameter and 4 to 6 cm long and collected small samples of skin and blubber approximately 3-4 cm long in calves and 4-6 cm in adults and juveniles. Skin and blubber biopsies were placed in plastic bags and preserved for up to three months in an insulated dewar flask filled with liquid nitrogen, and were later transferred to freezers at -80°C. For lipid content analysis skin biopsies were removed from the blubber.

Lipid content in blubber from dead and living calves

Procedures for preparation of blubber samples for lipid extraction were similar to those described by Ryan et al. (2013). Samples were weighed to approximately 0.5-1 gr (dead calf samples) and 0.30-0.60 gr (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 under two extraction methods in a Soxhlet apparatus: (a) hexane for 6 h and 9b) hexane for 6 h followed by soaking for 16 h. Because there were 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 h in Soxhlet envelopes, they were dried in a desiccator chamber for 24 h 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.

High and low mortality years

"High mortality" and "low mortality" years in the 2000s were defined following Marón et al. (2015a). Briefly, an exponential curve was fitted to the number of dead calves from 1971-2013 assuming the estimated annual growth rate of 6.8% (Cooke et al. 2003) and that the detection of dead calves by the SRWHMP was 1.75 times more efficient than the average efficiency during 1971-2002 (when the SRWHMP was not yet operational). Even with this generous assumption about the improvement in detection of dead calves by the SRWHMP, calf deaths in 2003, 2005 and 2007-13 were all significantly greater than expected (Marón et al. 2015a). The largest number of dead calves recorded in a low mortality year (2006) was 16 and the lowest number recorded in a high mortality year (2003) was 29 (Rowntree et al. 2013). Thus low mortality years in the 2000s were defined as those in which the number of dead calves was not significantly greater than expected (2004, 2006, 2014-2016) and high mortality years as those in which the number of dead calves was significantly greater than expected (2003, 2005 and 2007-2013).

Statistical analyses

Linear regression models for each of the nine blubber measurements were used to evaluate differences in blubber thickness of dead calves in relation to: (a) location (Golfo Nuevo or Golfo San José), (b) calf sex, (c) low or high mortality years. All models were adjusted for calf length and necropsy carcass condition as covariates. Analyses of variance (ANOVA) of linear models with and without interaction terms were contrasted to evaluate whether blubber thickness varied with the state of decay. Finally, ANOVA was used to ask whether the lipid content in the blubber of dead calves was significantly different from that of living calves. Variations in lipid content of blubber in dead calves of different lengths, states of decomposition or stranding year were also analyzed using linear regression models. All statistical analyses were conducted using in R version 3.3.1 (R Core Team 2016).

RESULTS

Blubber thickness increases with calf length

Both length and at least one blubber thickness measurement were recorded in 345 calves that died at Península Valdés from 2003 to 2017. 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, $0.47 \leq R^2 \leq 0.64$, all p-values < 0.001). The length of calves analyzed for blubber thickness ranged from 3.15 to 8.42 m. The minimum and maximum calf blubber thicknesses were measured at the dorsal-1 (blubber thickness: 0.70 cm, calf length: 4.17 m) and the ventral-3 sites (blubber thickness: 18.50 cm, calf length: 6.91 m), respectively.

Blubber thickness varies little with states of carcass decay

Controlling for calf length, carcass decomposition status had no significant effect on most blubber

thickness measurements among calves of similar size (ANOVA, *p*-values ranged from 0.15 to 0.79). However, blubber thickness at the dorsal-1 position varied among calves in condition codes 3 and 4 (ANOVA, $p = 0.05$). In consequence, calf length and state of decay were included as independent variables in all of the analyses described below.

Calves that died in high mortality years do not have thinner blubber than those that died in low mortality years

Controlling for calf length and state of decay, blubber thickness did not differ significantly among calves that died in high mortality years at eight out of nine blubber sites compared to low mortality years (Fig. 3). Blubber was thicker in high mortality years only at the lateral-1 position (regression, $p = 0.05$). More calves that died in high mortality years were large (> 6 m, n=277, 39%) compared to low mortality years (< 6 m, n=61, 21%).

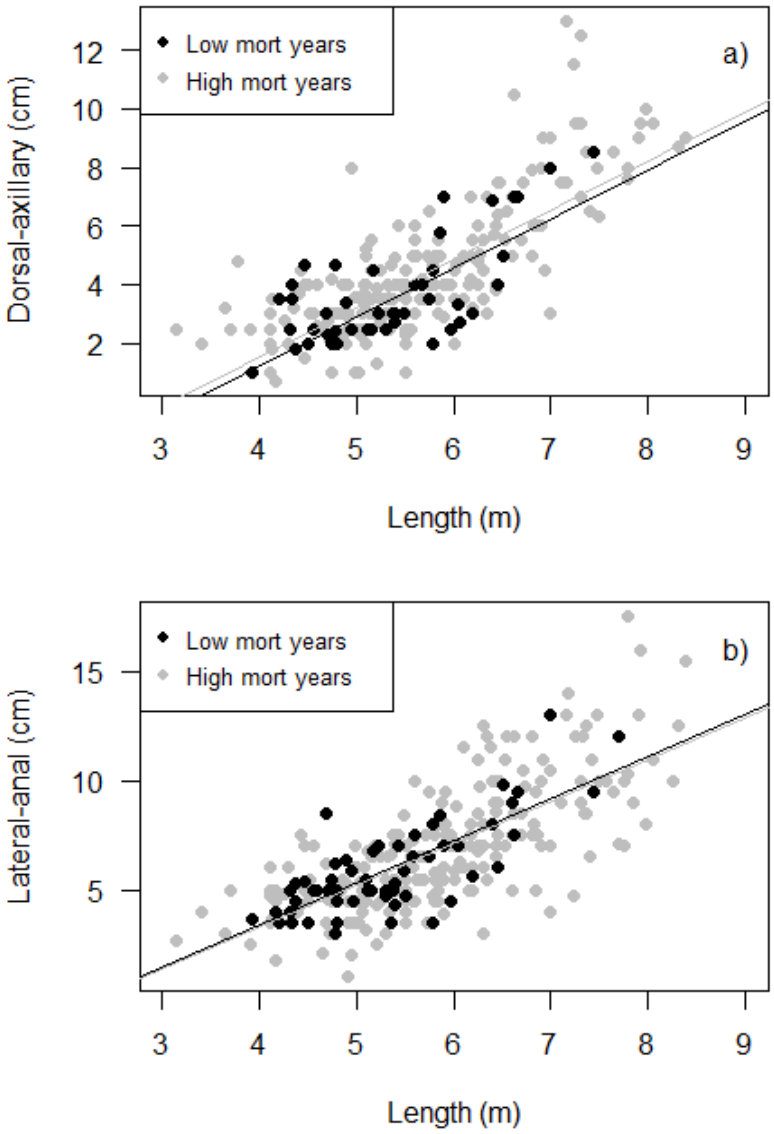

Fig. 3. Blubber thickness in relation to length for calves that stranded in low mortality (black dots) and high mortality (grey dots) years. Blubber thickness was taken in centimeters and length in meters. Parts a) and b) illustrate two out of nine blubber measurement locations, the dorsal-axillary (a) and lateral-anal (b) positions. Data were collected during necropsies from 2003 to 2017 at Península Valdés, Argentina.

Blubber thickness differs between stranding locations but not between sexes
Calves that died in Golfo Nuevo had thicker blubber than those dying in Golfo San José at six of the nine blubber thickness measurement sites (regression, *p*-values ranging from < 0.001 to 0.01).

Sex had no detectable effect on blubber thickness of dead calves at any of the nine sites (regression, p-values ranging from 0.13 to 0.85, with calf length and state of decay included as independent variables).

Lipid content of blubber does not differ between living and dead calves
Lipid content was analyzed in blubber samples from 67 calves that died at Península Valdés from 2009 to 2016 ($\overline{x}$ ± SD, 74% ± 9.57%) and in biopsy samples from 16 living calves biopsied in 2016 (76.72% ± 5.18%). Values from biopsy samples were within the range of lipid contents measured in blubber from the dead calves (ANOVA, $p = 0.28$). In dead calves, lipid content in blubber did not significantly vary with state of decomposition (fresh or moderate decomposition, ANOVA, *p*-values ranging from 0.11 to 0.87), length (regression, $p = 0.87$) or year (ANOVA, *p*-values ranging from 0.23 to 0.79).

DISCUSSION

The Península Valdés southern right whale population has experienced unusually high calf mortality events in recent years (Rowntree et al. 2013). Poor nutritional condition of mothers and calves has been proposed to explain this high calf mortality, but there have been no statistical analyses of body condition. Here we asked whether blubber thickness or the lipid content of blubber differed among calves that died in low- and high- mortality years and among living and dead calves. Contrary to expectation, we did not find differences in calf blubber thickness or lipid content that would implicate blubber fat storage as a factor contributing to deaths in high mortality years. Our sample sizes were large enough to provide statistical power to detect such effects. These negative findings therefore suggest that mechanisms other than nutritional stress may have played more important roles in the recent calf mortality events.

Blubber thickness increases with growth in many cetaceans (Lockyer 1991, Struntz & McLellan 2004, Miller et al. 2011, 2012). We found similar patterns in southern right whale calves at Península Valdés. Dead calves examined here ranged from neonates (< 6 m) to calves approaching 8.5 m. The blubber thickness of these dead calves increased with length in a manner similar to that of living and dead calves off South Africa (Reeb et al. 2007, Miller et al. 2011). A positive linear relationship of dorsal blubber thickness with body length was not found in living North Atlantic right whale calves (*E. glacialis*) (Miller et al. 2011), but only a small number of *E. glacialis* calves (n=9) could be measured and they represented a limited range of lengths (~8.5 to 10 m). Blubber thickness increased as well in southern right whale juveniles and adults harvested during illegal whale catches by the Soviet fleet in the 1960s (Tormosov et al. 1998) and in living North Atlantic right whale juveniles (Miller et al. 2011).

Blubber did not vary between in calves that died in low mortality years compared to calves that died in high mortality years. Furthermore, lipid content of blubber did not differ among living and dead calves of similar lengths. These findings do not support the hypothesis of reduced transfer of maternal fat reserves to calves in high mortality years. Moreover, data from the majority of calf necropsies at Valdés do not suggest debilitation or emaciation, regardless of calf mortality levels. In adult baleen whales, emaciation is evident through a reduction in dorsal blubber behind the blowholes that makes the scapula appear protruded and the lateral flanks depressed (Brownell & Weller 2001, Moore et al. 2001, Moore & Knowlton 2004, Bradford et al. 2008). We did not observe either of these anatomical features in the majority of dead calves. One recent study found that fat marrow content in the bones of dead calves at Península Valdés was low, however, this result is expected given their ages (McAloose et al. 2016). Lipid content can vary among blubber layers. Aguilar and Borrell (1990, 1991) found that the lipid content of the external blubber layer was more stable than that of the the more active inner layer, and did not vary with age and reproductive status in immature and mature mysticete whales. But other studies have found no significant differences in lipid content among blubber layers in adult baleen whales (Gauthier et al. 1997). No previous studies have analyzed variation in the lipid content of blubber in mysticete calves. In this study, we were only able to compared samples taken from the external blubber layer due to the logistical and ethical constraints against collecting deeper biopsy samples from living calves. Further studies should investigate variation in the lipid content of blubber among layers, body regions and throughout growth in baleen whale calves.

Blubber thickness did not change with carcass decomposition except for the dorsal-axillary blubber measurement site. Most calves found dead at Valdés are in advanced state of decay (condition code 4 or 5, Geraci and Lounsbury 2005) because an unknown period of time (rarely hours but mostly days or weeks) occurs between their deaths and their strandings and the subsequent necropsies (Uhart et al. 2008, 2009). Little is known about the effect of decay on blubber thickness in dead marine mammals. Gauthier et al. (1997) reported that the blubber thickness of a dead minke whale (*Balaenoptera acurostrata*) did not seem to vary when comparing samples taken 24 hours after death to samples taken one month after death. However, the lipid content of blubber, which seems more sensitive to degradation (Borrell & Aguilar 1990, Gulland & Hall 2005), decreased significantly during that same period. Our findings suggest that blubber thickness measurements may not be much by the state of decay of the whale, at least in calves in conditions 2 to 4.

Sex had no detectable association with the blubber thickness of calves. Sex has been shown to have a strong effect on the blubber reserves of adult living and dead whales (Lockyer 1981, 1986, 1987, Pettis et al. 2004, Miller et al. 2011), but 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,* (Lockyer 1995, Caon et al. 2007). In some species of baleen whales, adult females accumulate more blubber than adult males during certain phases of their reproductive cycles. Adult females have the thickest blubber prior to (Miller et al. 2011) and during pregnancy (Lockyer 1981, 1986, 1987) compared to juveniles, adult males and adult females in other reproductive stages (e.g., lactating females). Differential patterns of fattening were not detected in female and male calves in our study, an expected finding considering that it takes southern right whale calves a long time until they reach the blubber thickness of adults (Fig. 4 and Fig. 5 in Miller et al. 2011). However, in the harbor porpoise, blubber is thicker in female neonates compared to males, perhaps to favor female calf survival (Lockyer 1995). Current research in photogrammetry of southern right whale mothers and calves may shed light on changes in blubber thickness associated with sex during calf and juvenile growth.

Although we found no evidence of thinner blubber in calves that died during high mortality years *vs.* low mortality years, a nutritional factor cannot be ruled out as contributing to calf deaths. Many additional analyses, including lipid composition in blubber, body girths and urine metabolites, among others, could provide a more comprehensive picture of overall physical condition (Rice & Wolman 1971, Lockyer et al. 1985, Lockyer 1986, 1993, Caon et al. 2007). Ongoing nutritional (e.g., diet composition of mothers) and physiological (e.g., stress hormones in dead calves) analyses will supplement the findings presented in this study and provide a better understanding of underlying morbidity and / or debilitating processes. To date, no common cause has been found for the calf deaths at Valdés (Rowntree et al. 2013), although Kelp Gull attacks to eat the skin and blubber of living whales are unique to this calving ground and have drawn much attention as a potential contributor (Thomas et al. 2013, Marón et al. 2015b). Ongoing investigations should continue and new avenues for research must be explored to better assess the health of the Península Valdés southern right whale population.

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REFERENCES

Aguilar A, Borrell A (1990). Patterns of lipid content and stratification in the blubber of fin whales (*Balaenoptera physalus*). J of Mammal 71:544-554.

Aguilar A, Borrell A (1991). Heterogeneous distribution of organochlorine contaminants in the blubber of baleen whales: implications for sampling procedures. Mar Environ Res 31:275-286.

Borrell A, Aguilar A (1990) Loss of organochlorine compounds in the tissues of a decomposing stranded dolphin. Bull Environ Contam Toxicol 45:46–53.

Bradford A, Weller D, Ivashchenko Y, Burdin AM and others (2008) Seasonal and annual variation in body condition of western gray whales off northeastern Sakhalin Island, Russia. Scientific Committee of the International Whaling Commission's Document SC/60/BRG16, IWC, Cambridge.

Brown M, Kraus S, Gaskin D (1991) Reaction of North Atlantic right whales (*Eubalaena glacialis*) to skin biopsy sampling for genetic and pollutant analysis. Report of the IWC 13:81–90.

Brownell RJ, Weller D (2001) Is the "carrying capacity hypothesis" a plausible explanation for the "skinny" gray whale phenomenon? Scientific Committee of the International Whaling Commission's Document SC/53/BRG20, IWC, Cambridge.

Caon G, Fialho CB, Danilewicz D (2007) Body fat condition in franciscanas (*Pontoporia blainvillei*) in Rio Grande do Sul, southern Brazil. J Mammal 88:1335–1341.

Cooke J, 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. Scientific Committee of the International Whaling Commission's Document SC/55/023, IWC, Cambridge.

Dugail I, Guerre-Millo M (2009) Overview of the integrative physiology of adipose tissue in energy homeostasis. In: Frühbeck G (ed) Peptides in Energy Balance and Obesity: Frontiers in Nutritional Science. Vol 4. CABI Publishing, Cambridge, p 331–347.

Gauthier JM, Metcalfe CD, Sears R (1997) Validation of the blubber biopsy technique for monitoring of organochlorine contaminants in balaenopterid whales. Mar Environ Res 43:157–179.

Gulland F, Hall A (2005) The role of infectious disease in influencing status and trends. In: Reynolds JE III, Perrin W, Reeves R, Montgomery S, Ragen T (eds) Marine Mammal Research: conservation beyond crisis. Johns Hopkins University Press, Baltimore, p 47–62.

Gulland, F. M., Pérez-Cortés, H., Urgan, J., Rojas-Bracho, R. L., & Ylitalo, G. (2005). Eastern North Pacific gray whale (*Eschrichtius robustus*) unusual mortality event, 1999-2000 (pp. 1-33). US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center.

IWC (International Whaling Commision) (2011) Report of the Southern Right Whale die-off workshop. J Cetacean Res Manage (Suppl) 12:367–398.

Koopman HN, Pabst DA, McLellan WA, Dillaman RM and others (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. Physiol and Biochem Zool 75:498–512.

Kvadsheim PH, Folkow LP, Blix AS (1996) Thermal conductivity of minke whale blubber. J Therm Biol 21:123–128.

Lockyer C (1981) Growth and energy budgets of large baleen whales from the Southern Hemisphere. In: FAO Fisheries Series (eds), Mammals in the seas. Series 5, Vol III. FAO, Rome.

Lockyer C (1984) The biochemical composition of fin whale blubber. Can J Zool 62:2553–2562.

Lockyer C (1986) Body fat condition in northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. Can J Fish Aquat Sci 43:142–147.

Lockyer C (1987) Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. In: Huntley AC, Costa DP, Worthy GAJ, Castellini MA (eds) Approaches to Marine Mammal Energetics, Society of Marine Mammalogy Special Publication No. 1. Allen Press, Lawrence, KS, p 183–203.

Lockyer C (1991) Body composition of the sperm whale, *Physeter catodon*, with special reference to the possible functions of fat depots. Rit Fiskid 12:1–24.

Lockyer C (1993) Seasonal changes in body fat condition of northeast Atlantic pilot whales, and their biological significance. Report of the IWC 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 IWC 16: 199-210.

Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. J Mar Biol Assoc UK 87:1035–1045.

Lockyer CH, McConnell LC, Waters TD (1985) Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Can J Zool 63:2328–2338.

Marón CF, Rowntree VJ, Sironi M, Uhart M and others (2015a) Estimating population consequences of increased calf mortality in the southern right whales off Argentina. Scientific Committee of the International Whaling Commission's Document #SC/66a/BRG/1, IWC, Cambridge.

Marón CF, Beltramino L, Di Martino M, Chirife A and others (2015b) Increased wounding of southern right whale (*Eubalaena australis*) calves by Kelp Gulls (*Larus dominicanus*) at Península Valdés, Argentina. PLoS ONE 10(10):e0139291.

McAloose D, Rago MV, Di Martino M, Chirife A, and others (2016) Post-mortem findings in southern right whales Eubalaena australis at Península Valdés, Argentina, 2003-2012. Dis Aquat Org 119:17-36.

Miller C, Best PB, Perryman W, Baumgartner M and others (2012) Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. Mar Ecol Prog Ser 459:135–156.

Miller C, Reeb D, Best PB, Knowlton A and others (2011) Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. Mar Ecol Prog Ser 438:267–283.

Moore M, Knowlton A (2004) Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities. J Cetacean Res Manage 6:199–214.

Moore S, Urbán R. J, Perryman WL, Gulland F and others (2001) Are gray whales hitting "K" hard? Mar Mam Sci 17:954–958.

Oftedal OT (1993) The adaptation of milk secretion to the constraints of fasting in bears, seals, and baleen whales. J Dairy Sci 76:3234–3246.

Oftedal OT (2000) Use of maternal reserves as a lactation strategy in large mammals. In: Proc Nutr Soc 59(Suppl) 1:99–106.

Parry D (1949) The structure of whale blubber, and a discussion of its thermal properties. Q J Microsc Sci 3:13–25.

Pettis H, Rolland R, Hamilton PK, Brault S and others (2004) Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. Can J Zool 82:8–19.

Pond C (1978) Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. Annu Rev Ecol Evol Syst 9:519–570.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Reeb D, Best PB, Kidson SH (2007) Structure of the integument of southern right whales, *Eubalaena australis*. Anat Rec 290:596–613.

Rice DW, Wolman AA (1971) The life history and ecology of the gray whale (*Eschrichtius robustus*). Am Soc Mam, Spec Publication 3:27–37.

Rosen DAS, Winship AJ, Hoopes LA (2007) Thermal and digestive constraints to foraging behaviour in marine mammals. Phil Trans R Soc B 362:2151–2168.

Rowntree VJ, Uhart M, Sironi M, Chirife A and others (2013) Unexplained recurring high mortality of southern right whale *Eubalaena australis* calves at Península Valdés, Argentina. Mar Ecol Prog Ser 493:275–289.

Ryan C, McHugh B, O'Connor I, Berrow S (2013). Lipid content of blubber biopsies is not representative of blubber in situ for fin whales (*Balaenoptera physalus*). Marine Mammal Science 29:542-547.

Sironi M, Rowntree VJ, Di Martino M, Beltramino L and others (2014) Updated information for 2012-2013 on southern right whale mortalities at Península Valdés, Argentina. Scientific Committee of the International Whaling Commission's Document SC/65b/BRG06, IWC, Cambridge.

Sironi M, Rowntree VJ, Di Martino M, Beltramino L and others (2016). Southern right whale mortalities at Península Valdés, Argentina: updated information for 2014-2015. Scientific Committee of the International Whaling Commission's Document SC/66b/BRG/02, IWC, Cambridge.

Struntz D, McLellan W (2004) Blubber development in bottlenose dolphins (*Tursiops truncatus*). J Morphol 259:7–20.

Thomas PO, Uhart M, McAloose D, Sironi M and others (2013) Workshop on the southern right whale die-off at Península Valdés, Argentina. Scientific Committee of the International Whaling Commission's Document SC/60/BRG15, IWC, Cambridge.

Toedt M (2001) A histological and ultrastructural examination of the integument of *Delphinus delphis*. University of North Carolina.

Tormosov D, Mikhaliev Y, Best PB, Zemsky V and others (1998) Soviet catches of southern right whales *Eubalaena australis*, 1951–1971. Biological data and conservation implications. Biol Cons 86:185–197.

Uhart M, Rowntree VJ, Mohamed N, Pozzi L and others (2008) Strandings of southern right whales

(*Eubalaena australis*) at Península Valdés, Argentina from 2003-2007. Scientific Committee of the International Whaling Commission's Document SC/60/BRG15, IWC, Cambridge.

Uhart M, Rowntree VJ, Sironi M, Chirife A and others (2009) Continuing southern right whale mortality events at Península Valdés, Argentina. Scientific Committee of the International Whaling Commission's Document SC/61/BRG18, IWC, Cambridge.

Whitehead H, Payne R (1981) New techniques for assessing populations of right whales without killing them. In: FAO Fisheries Series (eds), Mammals in the seas. Series 5, Vol III. FAO, Rome.