FEEDING ECOLOGY, GULL HARASSMENT AND REPRODUCTIVE SUCCESS OF FEMALE SOUTHERN RIGHT WHALES

by

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ABSTRACT

Many factors can affect reproductive success in animals. In marine mammals, both nutritional and environmental stresses have been shown to influence maternal fertility and offspring survival. The southern right whales (*Eubalaena australis*) that calve off Península Valdés, Argentina, have experienced increased rates of calf death since 2003, but the cause(s) of this elevated mortality remain unknown. My research addresses the possible effects of diet and Kelp Gull harassment on the reproductive success of the whales. This study also provides novel insights into the diet composition, patterns of fattening, behavior, and reproductive life histories of right whales.

I first asked whether dead calves show a reduced proportion of fatty acids that are essential for calf growth, but I found no evidence to support this hypothesis. Then, I asked whether mothers of dead calves feed in different feeding grounds than mothers of living calves, but I found no significant differences among the two groups. Third, I investigated the diet composition of whales, and found that some mothers rely more than others on certain copepod species.

Next, I asked whether the body fat condition of calves worsens in years with high calf mortality, or in calves with more gull-inflicted lesions. I found no evidence to suggest a decline in the body fat condition of calves. Then, I evaluated how blubber thickness changes with calf growth and found that calves acquire a more streamlined body shape as they age.

I asked whether the incidence of gull-inflicted lesions in mothers and calves has increased in the 2000s (coincidentally with calf deaths). The numbers and areas of lesions in calves have increased greatly compared to mothers, suggesting that the health of nursing calves could be compromised if wounding continues to increase.

Finally, I investigated the occurrence of abnormal calving intervals and found that they increase significantly in years of high calf mortality compared to years of low mortality. I modeled the potential effects of a sustained increase in calf deaths and found that if elevated rates of calf mortality continue for some years, the population's growth could be slowed substantially.

To my family, friends and the whales.

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CHAPTER 1

INTRODUCTION

The reproductive success of an organism depends on many intrinsic and extrinsic factors. Nutritional and environmental stresses can contribute to reproductive failures if individuals cannot sustain both the energy demands of reproduction and self-maintenance under the effects of such stressors. In females of capital breeders, which depend on stored energy reserves to sustain reproduction (Stearns 1989), reproductive failures may occur if they are unable to accumulate enough reserves prior to breeding (Clutton-Brock 1988, Boutin 1990, Koskela et al. 1998). Baleen whales are capital breeders that gain fat during the feeding season and then migrate to their nursery ground to reproduce while fasting (Kellogg 1929, Townsend 1935, Nemoto 1970). This strategy of extreme feeding and fasting is very effective when it works, but it could lead to reproductive failures, when food becomes scarce on the whales' feeding grounds (Lockyer 1986, Leaper et al. 2006, Miller et al. 2011).

The southern right whale population that migrates to the Península Valdés calving ground in Argentina has experienced unusually high calf mortality events in recent years. At least 626 right whale calves died in 2003-2014, with no obvious common cause of death (Uhart et al. 2008, 2009, Rowntree et al. 2013, Sironi et al. 2014). Such large numbers of deaths are unusual for baleen whales, and several hypotheses, including poor nutritional condition of mothers, have been proposed to explain this high calf mortality (International Whaling Commision 2011). Nutritional stress could cause calving failures in the Valdés whales since there is evidence that mature females increased the proportion of abnormally long calving intervals following years of low Antarctic krill abundance (*Euphausia superba*, one of the whales' prey) (Leaper et al. 2006). Additionally, a more recent hypothesis considers high levels of Kelp Gull (*Larus dominicanus*) harassment as an environmental stressor contributing to calf deaths. Kelp Gulls are parasites of the whales at Valdés, feeding on their skin and blubber and affecting their normal behavior (Thomas 1988, Rowntree et al. 1998). To date, studies analyzing the body condition of the whales with respect to diet and gull harassment have been lacking. The Valdés right whale population represents a great study system in which to evaluate short- and long-term effects of nutritional and environmental stresses on reproduction, because the reproductive histories of individuals have been recorded continuously for forty-four years.

My dissertation research investigates the influence of diet and gull harassment on the reproductive success of southern right whales. Overall my results show that: a) calves that died during years of high calf mortality were not malnourished, b) the intensity of gull-inflicted lesions on calves has greatly increased in the 2000s, and c) the occurrence of abnormal calving intervals has increased in the reproductive histories of female whales in the 2000s coincidentally with calf deaths.

In Chapters 2 and 3, I evaluated whether dead calves show signs of malnutrition. In Chapter 2, I analyzed the fatty acid composition in the blubber of dead and living calves and found that length is the only factor explaining the differences among the two groups. Longer (and probably older) calves nurse for longer periods of time than shorter (younger) calves, and this influences their fatty acid composition. Stable isotope ratios in the skin of dead and living calves do not indicate that their mothers fed in different feeding grounds. I also used fatty acid analysis to infer the diet of the mothers and found that they vary, with some whales relying more heavily on calanoid consumption than others. In Chapter 3, I studied the blubber thickness of dead calves and found that blubber is overall thinner in low calf mortality years compared to high mortality years. I found no evidence to suggest that blubber thickness is reduced in calves with more gull-inflicted lesions. I also investigated how blubber thickness changes with length and found that calves acquire a streamlined shape with growth. These findings do not suggest a reduced transfer of fatty acids from mother to calf or a reduction in blubber reserves in calves that died in high mortality years.

Additionally, in Chapter 4, I analyzed the incidence of gull-inflicted lesions on mother-calf pairs. Gull lesions occurred in few whales in the 1970s but almost every mother-calf pair had lesions in the 2000s. Calves have almost twice the number of lesions as compared with mothers, and calves accumulate lesions throughout the season. Although I found no evidence of decreased blubber reserves with increased number of lesions on calves (Chapter 3), a sustained increase of wounding may compromise calf health (e.g., fatigue or stress) and thus contribute to the recent high calf mortality events observed in the 2000s.

Finally, in Chapter 5, I evaluated the occurrence of abnormal calving intervals using the 43-year photographic database of the Valdés right whale population and found that abnormal intervals increased in high mortality years in the 2000s. A mathematical model of the population predicted that if elevated rates of calf mortality continue for another decade or two, the population's growth is expected to slow substantially.

Overall, I found no evidence to support the poor-nutrition hypothesis as a direct cause of calf deaths. However, a nutritional factor cannot be ruled out as a contributor to calf mortality. Many other analyses, including lipid content in blubber, body girths, urine metabolites, and levels of stress hormones, among others, could provide a better understanding of the overall condition in the Valdés whales (Rice & Wolman 1971, Lockyer et al. 1985, Lockyer 1986, 1993, Caon et al. 2007). In addition, I found evidence to support that high levels of Kelp Gull harassment are occurring at Valdés, and that gull attacks have become more strongly focused on calves during the 2000s. The research presented here also provides a better understanding of the feeding ecology, behavior and reproductive life histories of southern right whales.

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CHAPTER 2

DIETARY DIVERSITY IN THE SOUTHERN RIGHT WHALE POPULATION OFF ARGENTINA INFERRED FROM FATTY ACIDS AND STABLE ISOTOPES

Abstract

Building fuel reserves is essential for animals that rely in their body fat (or protein) to sustain reproduction. This is the case for baleen whales that accumulate fat reserves during the summer to reproduce while fasting in the winter. The southern right whale (*Eubalaena australis*) population that calves off Península Valdés, Argentina, has experienced calving failures since 2003 and poor nutritional states of mothers could be a contributing cause. Previous studies found that the reproductive success of female whales is influenced by the availability of a key prey species, Antarctic krill (*Euphausia superba*). Thus if some mothers are unable to build enough fat reserves during the feeding season, they may not be able to meet the costly demands of lactation during the calving season. Here, we combined fatty acid (FA) and stable isotope analyses to investigate: 1) whether dead calves show a reduced proportion of FA that are essential for calf growth, as compared to living calves, 2) whether mothers of dead calves fed on different feeding grounds compared to mothers of living calves, and 3) whether the diet composition of living mothers varies. We found no evidence to suggest that the blubber of dead calves is depleted in essential FA and their derivatives. However, FA composition was greatly affected by calf length, with smaller (younger) calves showing FA compositions similar to gestational stages and larger (older) calves showing FA compositions influenced by milk consumption. The isotopic values of living and dead calves indicate that their mothers had fed at the same range of feeding locations. Mothers appear to feed on a variety of prey that may include krill and calanoid copepods. Some Valdés mothers rely heavily on calanoids (with elevated levels of the FA 20:1n-9 and 22:1n-11) while other whales forage more on other prey types. These findings do not suggest a reduced transfer of FA from mother to calf and thus a decline in the body condition of mother-calf pairs at Valdés. Further research is needed to assess the health and feeding ecology of the southern right whale population.

Introduction

Diet provides essential nutrients and energy to support self-maintenance and reproduction in all living organisms. Capital breeders have the capacity to accumulate energy reserves in their bodies that are later used to support reproduction during the breeding season (Stearns 1989). This is the case for baleen whales that increase their fat and protein energy reserves by feasting on prey in high-latitude feeding grounds during the summer, and then migrating to low-latitude calving grounds (where food is scarce) to calve during the winter. This strategy could become problematic when prey decline on the whales' feeding grounds. If whales are unable to accumulate enough fat reserves, then they may not meet the energy demands of reproduction, migration or even self-maintenance.

The southern right whale (*Eubalaena australis*) population that calves at Península Valdés, Argentina, increased at an average annual rate of 6.8% for several decades, but the estimated growth rate decreased to 5.1% in 2000-2010 (Cooke et al. 2003, Cooke 2012). Since 2003, large numbers of calves have died on the Valdés calving ground (at least 626 calves died in the period 2003-2014) (International Whaling Commision 2011, Sironi & Rowntree 2013, Sironi et al. 2014, Fig. 2.1). The cause(s) of the increased calf mortality remain unknown but poor nutritional state of mothers (International Whaling Commision 2011, Thomas et al. 2013) has been proposed as a contributor to the deaths since declines in Antarctic krill (*Euphausia superba*), a primary prey for the whales (Tormosov et al. 1998), have been correlated to reproductive failures. The Valdés females had fewer calves than expected following El Niño events when the abundance of Antarctic krill decreased in one of the whales' feeding grounds off South Georgia (Leaper et al. 2006). The whales also feed on calanoid copepods north of 40° S (Tormosov et al. 1998, Hoffmeyer et al. 2010); these prey items are much smaller in size and biomass compared to Antarctic krill (Brierley et al. 1999, Atkinson et al. 2001), but it is not known how reductions in the abundance of calanoid copepods affect southern right whale reproduction. If low prey abundance is affecting female reproductive success in the Valdés whales, then assessment of nutritional status of calves and its relationship to calf survival would be essential for understanding whether malnutrition is contributing to the recent high calf mortality events. In the present study, we used fatty acid and stable isotope analyses to assess maternal diet and feeding grounds, and to evaluate whether calves that die at Península Valdés show evidence of poor nutritional status.

Fatty acids (FA) and stable carbon and nitrogen isotopes have been used as biomarkers to study diet composition and feeding locations of marine mammals (Hooker et al. 2001, Herman et al. 2005, Budge, Wooller, et al. 2008, Krahn et al. 2008, Tucker et al. 2008). Both FA and stable isotopes are transferred from primary producers throughout the food web and deposited into animal tissues with predictable modifications (Wada et al. 1991, Iverson et al. 1995, 2004, Kirsch et al. 2000, Hooker et al. 2001, Bergé & Barnathan 2005, Budge et al. 2006). These techniques are particularly useful for studying the diets of species whose feeding cannot be observed directly. FA profiles (relative concentrations of all the FA identified in a sample) in the blubber of right whale mothers should reflect their diet composition since the FA obtained from their zooplanktonic food are allocated with little biochemical change into their blubber (Iverson 2009). Similarly, FA profiles in the blubber of right whale calves should reflect their nutritional status. If a mother's fat reserves are reduced due to low prey abundance, she might reduce milk output and thus compromise her calf's survival as has been demonstrated for other mammals (Oftedal 1985, Ono et al. 1987, Iverson 1993). Milk is the only source of energy for calves during their first three months of life at Península Valdés (Taber & Thomas 1982, Thomas & Taber 1984). Some FA such as 20:5n-3 and 22:6n-3 are derivatives from fatty acids that cannot be produced by animals and must be obtained from the diet (Christie 1982, Spector 1999, Das 2006). Both 20:5n-3 and 22:6n-3 must be transferred in adequate quantities during gestation and lactation for normal development of the mammalian offspring (Neuringer et al. 1984, Bourre et al. 1989, Cunnane et al. 2000, Uauy et al. 2001, McCann & Ames 2005).

Stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) can provide information about the diet and geographic range of a predator. Changes in the ratios of nitrogen and carbon in the predator tissues can be associated with changes in its diet and/or feeding locations (Hobson 1999, West et al. 2006). Stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) in the skin of the Valdés whales should reflect their feeding grounds. Valenzuela (2009) found distinct isotopic groups that may represent distinct feeding grounds of the Valdés whales: south of the Polar Front and around South Georgia, the Patagonian Sea and off the Uruguayan coast. Whaling records and direct observations indicate that whales may feed primarily on calanoid copepods north of 40° S at the Patagonian Sea (Tormosov et al. 1998, Hoffmeyer et al. 2010, Payne pers. comm.), and primarily on euphausiids south of 50° S, including South Georgia and the Polar Front (Lönnberg 1906, Matthews 1938, Hamner et al. 1988, Tormosov et al. 1998). This feeding pattern is likely explained by the fact that Antarctic krill are rarely found north of 50ºS (Atkinson et al. 2004, Nicol 2006). Isotope ratios of the Valdés calves should reflect their mothers' main feeding locations since there are small differences in nitrogen and carbon isotope ratios between mothers and calves (Valenzuela et al. 2010).

Here, we ask: (1) whether FA profiles in dead calves change with growth (length), sex, stranded location, survey years, years of low and high calf mortality, and carcass decomposition; (2) whether the FA profiles of dead and living calves indicate different nutritional status; (3) whether the FA profiles of living mother-calf pairs reflect transfer of FA from mother to calf; (4) whether maternal diets include a diversity of prey types; and 5) whether feeding locations differ between mothers of living and dead calves.

Materials and Methods

Blubber and Skin Samples from Dead Calves

Blubber samples were collected from southern right whale calves that died from June to December at Península Valdés (Golfo Nuevo and Golfo San José) in 2003-2011 (Fig. 2.1). Samples were used if they came from whales in states of decay “code 2” (fresh) and “code 3” (moderate decomposition) (Geraci & Lounsbury 2005). A full blubber sample with skin attached was removed from each whale at different body locations but mostly along the dorsal plane of the body (71%). FA composition is uniform across most body sites that share the same function (i.e., FA composition is similar in the fat that serves as energy storage but may differ from that in the fat that serves as structural blubber) (Koopman et al. 1996, Thiemann et al. 2006, Iverson et al. 2007, Budge et al. 2008). All blubber samples collected ranged in size from 5x5 to 15x15 cm. Blubber samples 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 make them comparable to blubber biopsy samples collected from living whales (which represent 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 just its middle section for lipid analysis. Skin samples were either frozen or preserved in ethanol for isotope analysis. Length (straight line from snout-tip to fluke notch), carcass decomposition, sex, date and location of necropsy were also recorded for each dead calf. Most necropsied calves died during high calf mortality years (2003, 2005, 2007-2011) when the number of calf deaths was significantly greater than expected. Fewer calves died in low mortality years (2004 and 2006) 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, see Chapter 5). Considering that calves are on average 5.5 m long at birth (Whitehead & Payne 1981), we defined small dead calves as those shorter than 6 m and large dead calves as those longer than 6 m.

Blubber and Skin Samples from Living Whales

Biopsy samples of skin and blubber from living mother-calf pairs and other noncalf whales were collected in 2011 at Golfo San José, Península Valdés, using darts propelled by a crossbow (Brown et al. 1991). Samples were taken dorsally, mainly at 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 removed 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 preserved for up to three months in an insulated dewar flask filled with liquid nitrogen, and were later transferred to freezers at -79°C.

Lipid Analysis

Blubber samples were lipid extracted with a 2:1 chloroform:methanol ratio following a modified Folch et al. (1957) procedure (Budge et al. 2006). Fatty acid methyl esters (FAME) were prepared from 1-10 mg of the extracted lipid (filtered and evaporated under nitrogen), using H_2SO_4 in methanol (Budge et al. 2006). FAME were extracted into hexane, concentrated, and brought up to a volume of 50 mg/mL with highpurity hexane. Analyses of FAME were performed according to Budge et al. (2006) by gas liquid chromatography using a GC2010 gas chromatograph (Shimadzu Scientific Instruments, Columbia, MD) fitted with a silica capillary column (30 m×0.25 mm ID) coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness; Agilent Technologies, DB-23; Palo Alto, CA, USA). A total of 58 FA were identified using the commercial calibration standard GLC-463 (Nu-Chek Prep, Elysian, MN). Each fatty acid is expressed as mass percent of total fatty acids and described using the nomenclature of carbon chain length:number of double bonds and location (n-x) of the double bond closest to the terminal methyl group. The total percentage of saturated (SA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids was also calculated.

Stable Isotope Analysis

To determine whether the mothers of dead calves fed in locations different from mothers of living calves, we compared stable isotopic values in dead and living calves. Stable nitrogen and carbon isotopes were measured in skin samples of dead (2003-2011) and living calves (2011) at SIRFER (Stable Isotope Ratio Facility for Environmental Research at the University of Utah). Skin samples were lyophilized and ground to a fine powder before lipid-extraction following Todd et al. (1997). Skin samples (~1mg) were analyzed using a Carlo Erba 1108 elemental analyzer coupled to a Thermo Finnigan Delta S Isotope Ratio Mass Spectrometer. Isotope ratios are expressed as $\delta^{13}C$ or $\delta^{15}N$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, for $\delta^{13}C$ or $\delta^{15}N$, respectively. Standards were referenced to Pee Dee Belemnite for carbon and to atmospheric air for nitrogen. The reproducibility of these measurements was 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ after repeated analyses of an internal laboratory standard (yeast and glutamic acid). The stable isotope ratios of 47 living calves determined by Valenzuela et al. (2010) in 2003-2005 were added to our analysis. We used 131 maternal isotopic values determined by Valenzuela et al. (2009) as a reference to compare with the ratios of calves.

Fatty Acid Data for Zooplankton

Information about FA composition in euphausiids and various species of Calanoid copepods distributed along the whales' feeding grounds (South Georgia, Polar Front and Antarctic Peninsula) was obtained from the literature. No data were found on the FA composition of calanoid copepods and euphausiids in the Patagonian Sea (other feeding ground for the whales). The estimated FA profiles of living mothers and other non-calves whales were compared to those from seven potential prey species using profiles from the literature (Antarctic krill *Euphausia superba,* and Calanoid copepods: *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus*, *Rhincalanus gigas, Metridia gerlachei,* and *Paraeuchaeta antarctica*). These zooplankton species employ different lipid metabolic pathways and thus they store a variety of saturated and/or monounsaturated FA, either associated with wax esters or triacylglycerols. For example, *C. acutus*, *C. propinquus* and *C. simillimus* contain in their lipid reserves high quantities of unusually long-chain monounsaturated FA such as the 22:1 isomers (Hagen & Auel 2001, Kattner et al. 2012). On the other hand, Antarctic krill, *R.gigas, M. gerlachei,* and *P. antarctica* accumulate a variety of different saturated and monounsaturated FA with 16 or 18 carbon atoms (Hagen & Auel 2001, Hagen et al. 2001). All of these zooplankton species are larger than

333 μm in their adult stages, which is the prey size fine baleen can efficiently trap (Mayo et al. 2001).

Statistical Analyses

To achieve normality, whale blubber FA data were transformed using the following function (Aitchison 1983): $x_t = \ln (x_i/c_r)$, where xt represents the transformed FA data, xi is a given FA expressed as percent of total FA and c_r is the percentage of a reference FA. We used 18:0 as the reference FA. To assess variation in the FA composition of calves with growth, principal components analysis (PCA) was performed on all 58 transformed FA using the FA profiles of dead calves. Repeated measures multivariate analysis of variance (MANOVA) was then carried out on the PC1 and PC2 scores with dead calf state of decay, survey year, calf mortality years (high or low), sex, and location as factors and body length (as a proxy for age) as a covariate. To assess variation in the nutritional status of calves, PCA was conducted on the 58 transformed FA using the FA profiles of living and dead calves. MANOVA was carried out on the PC1 and PC2 scores with calf length (small or large) and calf condition (dead or alive) as factors. These analyses were repeated in living and dead calves, using 18 transformed FA of predominantly dietary origin (Iverson et al. 2004), relatively high abundance, and high variance among individuals (14:0, 14:1n-7, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 18:2n-6, 18:3n-3, 18:4n-3, 20:1n-11, 20:1n-9, 20:4n3, 20:5n-3, 22:1n-11, 22:1n-9, 22:1n-7, 22:6n-3). Analysis of variance (ANOVA) was used to determine changes in the FA profiles of living mothers and their calves. To determine potential FA biomarkers for the whales' prey (Antarctic krill and calanoid copepods), PCA was conducted on ten transformed FA using the FA profiles found in the literature for the prey (14:0, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 20:1n-9, 20:5n-3, 22:1n-11, and 22:6n-3). The FA with the highest loadings on PC2 were selected as prey biomarkers. To determine whether the feeding grounds of mothers of living and dead calves differed, Kruskal–Wallis analysis of variance was used to test for differences of isotopic values between living and dead calves. All statistical analyses were conducted in R 3.1.0 (R Core Team 2013).

Results

Fatty Acid Composition in Southern Right Whales

A total of 58 FA were identified in the blubber of 72 living and dead southern right whales of different age classes, at average concentrations of 0.04% or more (Table 2.1). The major FA components (>1% of total FA) were dominated by 14:0, 14:1n-5, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 20:1n-9, 18:2n6, 18:4n3, 20:4n3, 20:5n-3, 22:5n-3, and 22:6n-3 in all age classes. The FA composition of small dead calves also showed other dominant FA such as 12:0, 16:1n-9, and 20:4n-6, and a reduction in the levels of 14:1n-5, 20:1n-9, and 18:4n-3 compared to the other age classes. FA profiles in adult and juvenile blubber was characterized by higher proportions of 20:1n-9 and 22:1n-11. The percentage of total MUFA was the highest in most age classes, followed by % PUFA and % SA. However, the proportion of SA was higher than the proportion of PUFA in small dead calves.

Fatty Acid Composition of Calves Changes with Growth

To evaluate whether FA profiles change with growth we compared the FA composition of four groups of whales: living mothers (*n*=14), living calves (*n*=13, usually larger than 6 m), small dead calves (*n*=40, smaller than 6 m) and large dead calves (*n*=11, larger than 6 m). Overall, the FA profiles of mothers differed from those of the calves, and small dead calves differed from the profiles of large dead and living calves (Table 2.1). In mothers, the isomers of 20:1 and 22:1 were very well represented in comparison to calves. Both isomers accounted for about 9.1% of the total FA in the mothers' blubber and only 1.5-3.3% in living and dead calves' blubber (Table 2.1). The FA 20:1n-9 was largely responsible for the higher percentage of MUFA found in mothers. In small dead calves, 12:0, 16:0 and 18:0 were higher compared to the levels found in the other three groups of whales. The saturated FA 16:0 was much higher in small dead calves and was responsible for the higher total percentage of saturated FA in this group compared to the others (Table 2.1). The MUFA 18:1n-7 showed also a higher concentration in small dead calves. The PUFA 20:5n-3, which comprised 8.95, and 9.09% of the large dead calves' and living calves' blubber, respectively, were found in smaller amounts in small dead calves (4.54%).

To assess variation in the FA composition of calves with growth, PCA of dead calves (large and small) was carried out on all 58 identified FA. Only dead calves were selected since their exact length was measured (range 3.64 to 8.05 m, 78% smaller than 6 m, Table 2.1). The first two PC explained 67% of the variance (PC1: 54%, PC2: 13%). The only factor that had a detectable effect on the FA composition of dead calves was length (Wilks' λ= 0.64, $p = 2.38\text{x}10^{-05}$). All other factors (high calf mortality vs. low calf mortality year, fresh vs. moderate state of decomposition, sex, location, and survey year) had no detectable effects on the FA profiles of dead calves (Wilks' λ for all these factors ranged from 0.96-0.99, and *p*-values ranged from 0.42-0.93). Percentages of total SA, total MUFA, total PUFA, the saturated FA 16:0, and the polyunsaturated FA 20:5n-3 and 22:6n-3 were compared with dead calf length. Both total SA and the FA 16:0 decreased with calf length (regression, SA% $p = 1.19\text{x}10^{-05}$, FA 16:0 $p < 0.001$). On the other hand, total MUFA, total PUFA and the FA 20:5n-3 and 22:6n-3 increased with length (regression, MUFA% $p = 0.01$, PUFA%, and FA 20:5n-3 and 22:6n-3 all *p*-values < 0.001). The levels of total MUFA, total PUFA and the FA 22:6n-3 seem to reach a plateau in calves larger than 6 m. However, the levels of 20:5n-3 increase even in calves longer than 6 m (Fig. 2.2).

Large Dead Calves Do Not Show Signs of Malnutrition

To assess variation in the nutritional status of calves, PCA of dead calves (large and small) and living calves was conducted on all 58 identified FA. This generated two PC that explained 72% of the variance (PC1: 55%, PC2: 17%, Fig. 2.3) with the saturated FA 18:0, which is higher in small dead calves, showing the highest loadings in PC1 and PC2. Living and large dead calves were clustered together and small dead calves showed a wider range of loadings. MANOVA was carried out using the PC1 and PC2 scores and a significant effect of length (shorter or longer than 6) was found when comparing living calves, small dead calves and large dead calves (Wilks' λ=0.54, $p < 0.001$). Additionally, the factor dead or alive had an effect when considering all calves (Wilks' λ=0.81, $p = 0.002$), but had no effect when analyzing only large dead calves and living calves (Wilks'

λ=0.99, $p = 0.93$). Similar results were found using just the 18 dietary FA (14:0, 14:1n-7, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 18:2n-6, 18:3n-3, 18:4n-3, 20:1n-11, 20:1n-9, 20:4n3, 20:5n-3, 22:1n-11, 22:1n-9, 22:1n-7, 22:6n-3) with 2 PC that explained 82% of the variance (PC1: 69%, PC2: 13%) and length continuing to affect the FA profiles of calves (Wilks' λ=0.55, $p < 0.001$).

Fatty Acid Profiles of Living Calves Show Evidence of Nursing

A total of nine living mother-calf pairs (*n*=18) were analyzed to evaluate FA transfer from mothers to calves. Fewer than half of the FA (41%) were significantly different among mothers and their calves (Table 2.2). Overall, the FA compositions of living calves differed from those previously reported for newborn of other marine mammals. The FA 14:0, 16:0, 14:1n-5, 16:1n-7, and 18:1n-9, which are overrepresented in the newborns of other marine mammals, were not higher in living southern right whale calves compared to their mothers (Table 2.3). The FA 14:1n-5 even showed significantly lower concentrations in calves than in mothers. Contrary to other marine-mammal newborns, the percentage of SA was not higher in calves than in their mothers, perhaps owing to the low levels of 14:0 and 16:0. Most 20:1 and 22:1 isomers were highly represented in mothers probably indicating calanoid copepod consumption. Calves had levels of these isomers only around one-third as high as their mothers. Percentages of MUFA were lower in calves and higher in mothers due to the large proportions of 20:1 and 22:1 isomers. On the other hand, levels of 20:5n-3 in calves were almost twice those in mothers. High levels of 20:5n-3 are characteristic of marine mammal suckling offspring. Also opposite to newborns, higher percentages of PUFA were found in calves' blubber, likely because of its high 20:5n-3 content.

Mothers Feed on a Varied Diet

FA compositions of potential whale prey were gathered from the literature to determine which FA can be used as biomarkers of Antarctic krill and calanoid copepods, respectively, and compared to the FA profiles found in the blubber of living mothers and other noncalf whales reported here. Data were found for potential prey on whale feeding grounds at South Georgia and Antarctica (Table 2.4), but not for the Patagonian Sea. The ten FA with the most data available included 14:0, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 20:1n-9, 20:5n-3, 22:1n-11, and 22:6n-3. PCA of these ten FA yielded two PC explaining 81% of the variance (PC1=60%, PC2=21%, Fig. 2.4). Except for 20:1n-9 and 22:1n-11, all of the FA had their highest loadings on PC1, which poses a difficulty for selecting a biomarker to separate Antarctic krill from copepods. However, 20:1n-9 and 22:1n-11 showed their highest loadings on PC2, with the copepods *C. acutus*, *C. propinquus* and *C. simillimus* having the highest concentrations of these FA compared to other copepods (*R. gigas*, *M. gerlachei*, and *P. antarctica*) and to the euphausiid *E. superba* (Table 2.4). Therefore, we used these two FA as biomarkers of copepods.

A total of 17 living whales were selected for comparing the FA profiles of potential prey and whales. Of these 17 whales, 14 were mothers, two were nonlactating adults (one male and one of undetermined sex), and one was a juvenile more than one year old. The FA patterns of the whales exhibited some similarities to that of Antarctic krill but also to two of the most dominant calanoid copepods in the Southern Ocean, *C. acutus* and *C. propinquus*. The FA 14:0, 16:0, 16:1n-7, and 18:1n-7 were highly represented in krill and the whales (Fig. 2.5). Comparing the concentrations of the two copepod biomarkers (20:1n-9 and 22:1n-11) in the whales and potential prey, we found that living whales showed a varied concentration of 20:1n-9 plus 22:1n-11 (range 1.3-14.6% of the total FA) that was overall lower to the values found in *C. acutus*, *C. propinquus* and *C. simillimus* (range 18.5-38.1% of the total FA) but higher than the values in the *R. gigas*, *M. gerlachei*, and *P. antarctica* and in the euphausiid *E. superba* (range 0.6-6% of the total FA, Fig. 2.6).

Feeding Grounds Do Not Differ Among Mothers of Living and Dead Calves

Stable carbon and nitrogen ratios were analyzed in the skin of 58 dead calves and 89 living calves (47 of which were previously determined by Valenzuela et al. 2010) to assess the whales' potential feeding grounds. Samples were obtained in different time periods: 2003-06 for living mothers, 2003-05 and '11 for living calves, and 2003-06 for dead calves. All the samples from living whales were collected in Golfo San José, but the samples from dead calves were collected in both Golfo San José (26%, *n*=15) and Golfo Nuevo (72%, *n*=43). The stable carbon and nitrogen isotope values of living and dead calves showed a wide range of values. $\delta^{13}C$ ranged from –23.8 to –16.9‰ (mean = –21.6‰, SD = 1.5‰) in living calves and from –23.7 to –16.9‰ (mean = –21.8‰, SD = 1.6‰) in dead calves. $\delta^{15}N$ ranged from 6.7 to 14.1‰ (mean = 8.3‰, SD = 1.6‰) in living calves and from 5.9 to 14.1‰ (mean = 8.3‰, SD = 2.0‰) in dead calves. Mean $\delta^{13}C$ and δ15N values did not differ among living and dead calves (Kruskal–Wallis $\delta^{13}C$: $\chi^2 = 1.08$; $p = 0.3$, and $\delta^{15}N$: $\chi^2 = 0.6$; $p = 0.8$). The stable isotope ratios of living and dead calves were plotted together with the isotopic values of 131 living mothers (all of them determined by Valenzuela et al. 2009, Fig. 2.7). The isotopic range of the calves corresponds to the three isotopic groups recognized by Valenzuela et al. (2009) that may represent the whales' feeding grounds at South Georgia and the Polar Front, the Patagonian Sea, and the Uruguayan coast.

Discussion

Assessing the diet and nutritional status of marine mammals can be challenging for species that forage on remote feeding grounds. Very little is known about diet of southern right whales and most of our knowledge is derived from analysis of stomach contents of whales harvested during illegal whaling (Matthews 1938, Tormosov et al. 1998), sporadic observations of individuals foraging on their feeding and calving grounds (Hamner et al. 1988, Hoffmeyer et al. 2010, Payne per. comm.), and indirectly from stable isotope analysis (Rowntree et al. 2008, Valenzuela et al. 2009). This study attempts to combine FA and stable isotope analyses to better understand the feeding ecology and nutritional status of the southern right whales off Península Valdés. Our main findings suggest that the whales have a mixed diet with variable dependence on calanoid copepods, and that dead calves do not appear to have suffered reduced deposition of essential and nonessential FA in their blubber due to lower maternal milk output during high calf mortality years.

The FA composition of southern right whales is typical for marine mammals. Their profiles include FA with 12-24 carbon atoms and higher percentages of MUFA, followed by % PUFA and % SA for most age whale classes. In small dead calves, however, % SA was the second most abundant group of FA. Six major FA accounted for around 60% of the whale blubber in all age classes: 14:0, 16:0, 16:1n-7, 20:5n-3, 22:5n-3, and 22:6n-3. The FA 20:1n-9 and 22:1n-11 were also predominant components, but only in the adult and juvenile blubber.

These proportions differ to some extent from those of southern right whales off South Africa. Around 13 FA were identified in the blubber of these whales with saturated FA as the second most abundant group in all age classes and the isomers 20:1, 22:5 and 22:6 showing lower levels in mothers compared to our results (Reeb 2001). The PUFA 20:5n-3, which was found in higher concentrations in the Valdés whales, was not identified in the whales off South Africa. These differences may result from different protocols for FA analysis and sample collection in the two studies. The capillary columns used in the South Africa study produced chromatograms where only 13 major FA could be identified. Following the recommendations to analyze lipids in marine mammals (Budge et al. 2006), we used a polar capillary column that allowed us to identify 58 FA and to separate important FA such as 20:1n-9 and 22:1n-11 (biomarkers of copepods) and the many isomers of long-chain PUFA such as 20:5n-3 (crucial for calf development).

For the whales off South Africa, FA profiles of living individuals were determined using a combination of samples taken from the inner (close to the muscle), middle and outer layers (close to the skin) of the blubber. Because FA composition in cetaceans could change with depth in the blubber layer, it is recommended to compare samples taken from the same depth. To avoid FA stratification issues, we compared only samples taken from the outer layer. However, the outer layer is less rapidly influenced by changes in diet and the use of a more active inner layer would be preferable for studies of diet in cetaceans (Cooper 2004, Iverson et al. 2004). In the present study we collected samples from the outer blubber of living individuals and therefore needed to compare those samples with the outer layer from dead whales. A sophisticated technique has been developed to collect deep blubber samples from living southern right whales, but this technique has been tested only in the whale population off South Africa (Reeb & Best 2006).

FA composition of calves changes with growth. In small calves, the prevalence in the total percentage of saturated FA is explained by higher proportions of 12:0, 16:0 and 18:0. The proportion of 16:0 was particularly higher in small calves (<6 m in length) as is typical of newborn marine mammals (Iverson et al. 1995, Birkeland et al. 2005). This saturated FA is proposed to be produced by the offspring during gestation through the action of FA synthetase (Iverson et al. 1995, Birkeland et al. 2005). The FA 18:1n-7 also showed higher concentrations in small calves and it is known to be highly concentrated in the blubber of newborns (Iverson et al. 1995, Birkeland et al. 2005, Wheatley et al. 2008).

In large calves, the total percentages of MUFA and PUFA increased with length, particularly the proportions of the PUFA 20:5n-3 and 22:6n-3 when compared to the levels found in small calves. There is evidence of a selective mobilization of 20:5n-3 and 22:6n-3 through maternal milk which results in accumulation of these FA in the blubber of the offspring throughout lactation (Iverson et al. 1995, Grahl-Nielsen et al. 2000, Wheatley et al. 2008). Both FA play a role in the development of the circulatory and neurological systems in many animals (Neuringer et al. 1984, Bourre et al. 1989, Bell et al. 1995, Cunnane et al. 2000, Uauy et al. 2001, McCann & Ames 2005), making it likely that higher concentrations of these FA in the calves' blubber may be required for enhancing calf growth. Similar results were found in the southern right whale calves off South Africa. Calves decrease the proportion of total SA and increase total MUFA from earlier to later in the season (Reeb 2001).

It has been hypothesized (Reeb 2001) that differences in the FA profiles of small and large calves are due to differential times of nursing. Small (younger) calves might not have enough time to nurse as long as large (older) calves and their FA reflect a profile more similar to gestational stages (with prevalence of saturated FA) than to the profiles influenced by milk consumption (with prevalence of 20:5n-3, 22:6n-3, other PUFA, and MUFA) typical of large calves. The distribution of FA profiles in small calves (Fig. 2.3), may also reflect a differential nursing period among individuals within this group. Small dead calves that clustered much closer to the profiles of living calves and large dead calves may have been nursing for a longer period of time than calves that were distributed away from those profiles. Thus FA analysis may indeed serve as a useful tool to determine age in calves. Although length can be used as a proxy of age in calves, it may not be as useful for differentiating the age of calves that actually have the same lengths but were born at different times and at different lengths (Best & Rüther 1992). Primiparous females usually give birth to small calves compared to multiparous females. FA analysis has been successfully used to determine the age of juvenile and adult humpback and killer whales (Herman et al. 2008, 2009). In this study, we provide some evidence that suggests that FA can be used as a more accurate indicator of calf age even in a very small window of time (months) since the profiles of small calves were very different from large calves which were not more than 4 months old (mothers stay at

Valdés for up to 4 months, Thomas & Taber 1984).

FA composition of dead calves showed no evidence of FA deficiency. Significant differences were not found among the FA profiles of dead calves and living calves of similar size (>6 m). Important FA such as 20:5n-3 and 22:6n-3, which are required for the normal development of the young in many animals (Neuringer et al. 1984, Cunnane et al. 2000, Uauy et al. 2001, Innis 2007), showed almost identical values in both living and large dead calves. Controlling for length, the FA profiles of calves that died in low mortality years were similar to the profiles of calves that died in high mortality years. We were unable to compare small dead calves with small living calves (<6 m) since we only biopsied large living calves. However, the FA values of small dead calves were similar to the values found in newborns of other marine mammals (Iverson et al. 1995, Grahl-Nielsen et al. 2000, Birkeland et al. 2005, Wheatley et al. 2008) indicating that they might have nursed for a short period of time. The essential FA 18:2n-6 and 18:3n-3, that cannot be biosynthesized by animals and need to be incorporated from the diet, and their PUFA derivatives (including 20:5n-3 and 22:6n-3) were not depleted in the blubber of dead calves. Depletion of PUFA and increase of short-chain saturated and short-chain MUFA has been found in malnourished humans compared to well-nourished individuals (Holman et al. 1995). It has been also shown that FA composition significantly changes between feed-restricted and well-fed animals (Allmann et al. 1965, Jezierska et al. 1982, Kirsch et al. 2000). Our findings suggest that maternal transfer of FA was not limited during years of high calf mortality.

Living calves have FA profiles similar to those of other of suckling marine mammals. Most FA profiles in the blubber of fetus and newborn marine mammals are dominated by large amounts of saturated FA (14:0, 16:0) and MUFA (14:1n-5, 16:1n-7, 18:1n-9) in concentrations that greatly exceed those found in their mothers. Newborns also have low levels of PUFA and the levels of 20:5n-3 are usually low since this PUFA is selectively transferred through maternal milk (Iverson et al. 1995, Grahl-Nielsen et al. 2000, Birkeland et al. 2005, Wheatley et al. 2008). Living southern right whale calves overall did not show higher concentrations of saturated and monounsaturated FA compared to their mothers. Additionally, the levels of PUFA were significantly higher in calves than their mothers, especially for 20:5n-3 that was nearly twice as abundant as in the maternal blubber. Opposite to mothers, most 20:1 and 22:1 isomers were underrepresented in the blubber of living calves. The isomers of 20:1 and 22:1 have also been shown to be underrepresented in the offspring of other marine mammals but their levels increase through lactation (Iverson et al. 1995, Birkeland et al. 2005, Wheatley et al. 2008). The FA 20:1n-9 and 22:1n-11 mainly originate from the diet and are trophic markers for calanoid copepods.

Southern right whale mothers feed on a varied diet at different feeding grounds. Similarities between the FA profiles of whales and their potential prey were not obvious (Fig. 2.5). Whales could be obtaining large amounts of 16:1n-7, 18:1n-9 and 18:1n-7 from Antarctic krill, but these FA are not unique markers of krill and can be biosynthesized as storage lipids in other less abundant zooplankton species (*R. gigas*, *M. gerlachei*, *P. antarctica*, and other euphausiids not included in this study including *E. crystallorophias* and *Thysanoessa macrura*, all inhabitants of Antarctic waters, Hagen & Auel 2001). These FA can also be produced by the whales. Another option to assess diet is to use some PUFA as biomarkers instead of the entire FA profile. PUFA are more elaborate FA that require more elongation and desaturation than the more simple saturated or monounsaturated FA with 16 or 18 carbons. Although 20:5n-3 and 22:6n-3 are elaborated PUFA with larger concentrations in Antarctic krill (Hagen & Auel 2001) they cannot be used as diet biomarkers since their concentrations are also high in calanoid copepods (Table 2.4, Fig. 2.5). However, the MUFA 22:1n-11 and 20:1n-9 are storage fat largely produced by some calanoid copepods such as *C. acutus*, *C. propinquus,* and *C. simillimus* (Table 2.4, Hagen et al. 1993, Kattner et al. 1994, Ward et al. 1996) and can be used as biomarkers of copepod consumption (Sargent & Henderson 1986). Most Valdés right whales showed higher concentrations of these FA compared to Antarctic krill and the copepods *R. gigas*, *M. gerlachei*, *P. antarctica,* but lower concentrations compared to *C. acutus*, *C. propinquus,* and *C. simillimus*. Some whales seem to feed more intensively on calanoid copepods than whales with lower concentrations of these biomarkers (22:1n-11 + 20:1n-9 ranged from 1.3 to 14.6% in the whales). Although there is no published data about the FA composition in copepods of the Patagonian Sea, *C. propinquus,* and *C. simillimus* also occur at the Patagonian Sea (Ramírez 1981, Ramírez & Sabatini 2000, Antacli et al. 2014) and might potentially accumulate large quantities of 22:1n-11 and 20:1n-9 like their counterparts in Antarctica (Table 2.4, Fig. 2.5). Thus it is likely that the Valdés whales feed on calanoid copepods along the Patagonian Sea (Tormosov et al. 1998) and/or in Antarctic waters. The diet of the North Pacific right whale (*Eubalaena japonica*) is characterized by large quantities of copepods and small quantities of euphausiids (Klumov 1962). Around 20% of the blubber of these whales is dominated by the 20:1 and 22:1 biomarkers (Tsuyuki & Itoh). The western Arctic bowhead whales (*Balaena mysticetus*) rely heavily on copepods and FA composition analyses indicate high concentrations of 20:1 and 22:1 isomers in these whales (Budge et al. 2008). By comparison, a southern right whale with ~15% of these FA in its blubber may have fed on large quantities of calanoid copepods. *Calanus propinquus*, an abundant calanoid copepod in Antarctica (Marin & Schnack-Schiel 1993, Schnack-Schiel & Hagen 1995) and the Patagonian Sea (Ramírez 1981) and with high concentrations of 20:1 and 22:1, has been identified in the stomach content of southern right whales illegally harvested in the South Atlantic during the 1960s (Tormosov et al. 1998). Our data confirm that southern right whales rely to a greater or lesser extent on calanoid copepods as a source of nutrients and energy.

Stable isotope ratios in the skin of living and dead calves suggest that their mothers fed on a similar range of feeding grounds. Valenzuela et al. (2009) recognized distinct stable isotope ratios in the Valdés right whale mothers, with some groups apparently feeding at South Georgia and the Polar Front, and other groups feeding closer to the Patagonian Sea and Uruguayan coast. The lowest and highest isotopic values that we found in living and dead calves fall within the same range indicating that their mothers had similar foraging distributions and fed on similar prey.

Although we found no evidence to support the hypothesis that mothers of dead calves were relatively malnourished, a nutritional factor cannot be excluded as a potential contributor to the calf deaths. Other studies need to be undertaken, such as the evaluation of anatomical, physiological and behavioral condition of calves, in order to evaluate the overall health of the Valdés right whale population. Further research should examine how FA composition changes with body locations, blubber depth, and whale age, sex and reproductive status. Our findings show that data for such studies can be collected from living or from dead whales in fresh or moderate states of decay. Additionally, the FA composition of the very abundant calanoid copepods and other zooplankton species that inhabit the Patagonian Sea should be documented. The Patagonian Sea is an important feeding ground not only for the whales, also for many species of fish, birds and mammals. The FA profiles of the Patagonian copepods will illuminate the diet and migration patterns of the Valdés right whales.

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Table 2.1. Fatty acid composition (mean and standard error) in living and dead southern right whales. Small dead calves and large dead and living calves indicate individuals smaller or larger than 6 m long.

Fatty acid	**Living mothers**		**Small dead calves**		**Large dead calves**		**Large living calves**		**Living juvenile and adults**	
	n=14		*n*=40		*n*=11		*n*=13		*n*=3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Saturated										
C12:0	0.09	0.00	2.48	0.82	0.12	0.02	0.09	0.00	0.08	0.00
C13:0	0.08	0.03	0.15	0.02	0.05	0.01	0.04	0.00	0.05	0.01
C14:0	6.18	0.18	5.54	0.38	6.04	0.24	5.92	0.19	6.27	0.40
i-15:0	0.28	0.05	0.25	0.03	0.22	0.02	0.23	0.05	0.20	0.01
ai-15:0	0.11	0.02	0.06	0.01	0.07	0.00	0.07	0.00	0.08	0.01
C15:0	0.43	0.02	0.33	0.01	0.35	0.02	0.34	0.01	0.37	0.01
i-16:0	0.14	0.02	0.63	0.12	0.22	0.12	0.10	0.01	0.12	0.01
C16:0	9.48	0.47	16.07	0.84	10.83	0.48	10.61	0.26	10.21	0.27
i-17:0	0.27	0.01	0.23	0.01	0.24	0.01	0.27	0.01	0.29	0.01
ai-17:0	0.15	0.01	0.23	0.04	0.13	0.01	0.13	0.01	0.13	0.01
C17:0	0.19	0.01	0.23	0.01	0.22	0.02	0.21	0.01	0.18	0.02
C18:0	1.72	0.07	5.72	0.47	2.65	0.34	2.66	0.16	1.98	0.18
C20:0	0.13	0.01	0.23	0.02	0.10	0.02	0.09	0.01	0.12	0.02
Subtotal	19.25	0.65	32.17	1.49	21.24	0.75	20.75	0.47	20.08	0.43
Monounsaturated										
C14:1n-9	0.26	0.06	0.14	0.01	0.12	0.01	0.13	0.01	0.14	0.03
C14:1n-7	0.11	0.04	0.10	0.01	0.06	0.00	0.07	0.01	0.06	0.01
C14:1n-5	1.57	0.06	0.85	0.04	1.07	0.06	1.11	0.06	1.47	0.14
C16:1n-11	0.46	0.02	0.29	0.04	0.38	0.03	0.46	0.09	0.45	0.02

Table 2.1. Continued

Fatty acid	**Living mothers**		**Small dead calves**		**Large dead calves**		**Large living calves**		**Living juvenile and adults**	
	n=14		*n*=40		*n*=11		*n*=13		*n*=3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
C16:1n-9	0.33	0.02	1.10	0.13	0.36	0.07	0.39	0.07	0.30	0.02
C16:1n-7	14.97	0.91	12.71	0.52	15.63	0.90	15.83	0.69	15.87	1.17
C16:1n-5	0.29	0.01	0.29	0.01	0.29	0.01	0.28	0.01	0.31	0.02
C17:1	0.09	0.02	0.07	0.00	0.06	0.00	0.07	0.00	0.07	0.01
C18:1n-11	0.77	0.09	0.64	0.10	0.51	0.12	0.38	0.07	0.44	0.08
C18:1n-9	19.43	0.60	17.62	0.41	19.17	0.33	19.98	0.37	19.73	1.04
C18:1n-7	3.99	0.34	7.08	0.34	5.66	0.57	5.86	0.35	4.82	0.94
C18:1n-5	0.67	0.10	0.79	0.05	0.56	0.06	0.50	0.04	0.53	0.09
C20:1n-15	0.08	0.00	0.05	0.01	0.05	0.00	0.07	0.01	0.07	0.01
C20:1n-11	0.85	0.08	0.22	0.01	0.32	0.07	0.24	0.02	0.53	0.18
C20:1n-9	6.34	1.01	0.92	0.10	2.12	0.46	1.51	0.21	3.89	0.69
C20:1n-7	0.43	0.09	0.50	0.04	0.25	0.04	0.24	0.02	0.30	0.02
C22:1n-11	1.50	0.24	0.27	0.03	0.61	0.18	0.31	0.05	1.18	0.24
C22:1n-9	0.43	0.05	0.23	0.02	0.24	0.03	0.20	0.02	0.32	0.02
C22:1n-7	0.07	0.01	0.09	0.01	0.04	0.01	0.06	0.01	0.07	0.01
C24:1	0.26	0.05	0.18	0.03	0.12	0.03	0.17	0.02	0.23	0.06
Subtotal	52.89	0.82	44.14	0.77	47.64	0.45	47.86	0.60	50.78	2.71
Polyunsaturated										
C16:2n-6	0.10	0.01	0.08	0.01	0.05	0.00	0.05	0.00	0.07	0.01
C16:2n-4	0.42	0.02	0.29	0.03	0.50	0.04	0.48	0.02	0.44	0.05
C16:3n-4	0.45	0.02	0.27	0.02	0.41	0.02	0.42	0.01	0.45	0.04
C16:4n-3	0.41	0.07	0.21	0.02	0.29	0.02	0.35	0.02	0.37	0.03

Table 2.1. Continued

Fatty acid	**Living mothers**		**Small dead calves**		**Large dead calves**		**Large living calves**		**Living juvenile and adults**	
	n=14		*n*=40		*n*=11		*n*=13		*n*=3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
C16:4n-1	0.19	0.02	0.09	0.01	0.12	0.01	0.11	0.01	0.18	0.05
C18:2n-6	1.83	0.04	1.35	0.12	1.80	0.07	1.94	0.05	1.98	0.05
C18:2n-4	0.10	0.02	0.14	0.01	0.12	0.01	0.11	0.01	0.09	0.00
C18:3 n-6	0.16	0.02	0.09	0.01	0.11	0.01	0.11	0.01	0.14	0.02
C18:3n-4	0.22	0.01	0.17	0.01	0.20	0.02	0.17	0.01	0.18	0.02
C18:3 n-3	0.92	0.05	0.54	0.07	0.93	0.08	0.88	0.04	0.96	0.14
C18:3n-1	0.10	0.01	0.10	0.01	0.06	0.01	0.06	0.00	0.08	0.00
C18:4n-3	1.74	0.20	0.51	0.08	1.08	0.19	1.14	0.13	1.61	0.20
C18:4n-1	0.23	0.02	0.33	0.03	0.49	0.03	0.46	0.03	0.29	0.08
C20:2n-6	0.26	0.01	1.00	0.12	0.34	0.14	0.28	0.03	0.26	0.03
C20:3n-6	0.17	0.01	0.41	0.04	0.23	0.02	0.23	0.01	0.20	0.01
C20:4 n-6	0.46	0.03	1.10	0.16	0.70	0.17	0.65	0.03	0.55	0.05
C20:3n-3	0.18	0.02	0.07	0.01	0.13	0.02	0.13	0.01	0.17	0.01
C20:4n-3	1.82	0.12	1.19	0.16	2.31	0.22	2.25	0.12	1.73	0.09
C20:5n-3	4.95	0.25	4.54	0.44	8.95	0.74	9.09	0.45	6.95	1.37
C21:5n-3	0.37	0.03	0.53	0.03	0.41	0.03	0.42	0.02	0.34	0.06
C22:4n-6	0.18	0.02	0.28	0.03	0.13	0.02	0.17	0.03	0.16	0.02
C22:5n-6	0.35	0.03	0.17	0.02	0.14	0.02	0.21	0.04	0.27	0.08
C22:4n-3	0.33	0.04	0.21	0.02	0.21	0.03	0.27	0.04	0.26	0.02
C22:5 n-3	3.22	0.18	5.50	0.23	4.70	0.31	4.76	0.22	3.51	0.69
C22:6n-3	8.70	0.24	4.54	0.31	6.71	0.46	6.66	0.34	7.87	0.49
Subtotal	27.86	0.51	23.69	1.05	31.12	0.63	31.39	0.53	29.13	2.29
Total	100		100		100		100		100	

Table 2.2. Composition of blubber fatty acids of southern right whale mother-calf pairs (*n*=9). Each ratio represents the average ratio of all mother-calf pairs. Values are weight % of total fatty acids. Only significant values are shown (ANOVA, $p \leq 0.05$). Fatty acids in bold indicate higher concentrations in calves compared to their mothers.

Fatty acid	**Ratio calf: mother**	**p-value**
12:0	1.04	
13:0	0.79	
14:0	0.96	
14:1n-9	0.76	
14:1n-7	1.1	
14:1n-5	0.7	0.0002
i-15:0	1.43	
ai-15:0	0.75	0.001
15:0	0.84	0.009
i-16:0	0.86	
16:0	1.13	
16:1n-11	1.17	
16:1n-9	1.39	
16:1n-7	1.03	
16:1n-5	0.97	
i-17:0	1.05	
16:2n-6	0.55	0.0002
ai-17:0	0.92	
16:2n-4	1.09	
C17:0	**1.29**	**0.03**
16:3n-4	0.98	
17:1	1.15	
16:4n-3	1.09	
16:4n-1	0.69	0.02
18:0	**1.63**	**0.0003**
18:1n-11	0.86	
18:1n-9	1.03	
18:1n-7	**1.54**	**0.02**
18:1n-5	0.93	
18:2n-6	1.06	
18:2n-4	1.16	
18:3n-6	0.75	

Table 2.2. Continued

Fatty acid	**Ratio calf: mother**	**p-value**
18:3n-4	0.81	0.05
18:3n-3	0.96	
18:3n-1	0.63	0.002
18:4n-3	0.74	
18:4n-1	**2.04**	**< 0.001**
20:0	0.76	0.007
20:1n-15	0.89	0.007
20:1n-11	0.34	< 0.001
20:1n-9	0.31	0.006
20:1n-7	0.72	0.05
20:2n-6	1.22	
20:3n-6	1.28	
20:4n-6	**1.45**	**0.02**
20:3n-3	0.82	
20:4n-3	1.49	
20:5n-3	**1.79**	**< 0.001**
22:1n-11	0.29	0.006
22:1n-9	0.52	0.006
22:1n-7	1.03	
21:5n-3	2.17	
22:4n-6	1.18	
22:5n-6	0.76	
22:4n-3	1.19	
22:5n-3	**1.49**	**0.002**
22:6n-3	0.84	0.01
24:1	0.93	
SA	1.1	
MUFA	0.91	0.003
PUFA	**1.14**	**0.002**

Table 2.3. Composition of blubber fatty acids of hooded seal (*Cystophora cristata*), white whale (*Delphinapterus leucas*), and southern right whale mothers and offspring. In the hooded seal, the ratio represents the fatty acids of a mother in comparison to that of her pup at birth prior to nursing. Blubber samples were taken from the entire blubber layer. In the white whale, the ratio represents the average fatty acids proportions of four mothers in comparison to one calf of an estimated age of less than one week old. Blubber samples were taken from the inner blubber layer. In the southern right whale, the ratio represents the average ratio of nine mother-calf pairs. Blubber samples were taken from the outer layer. Values are weight % of total fatty acids.

	Ratio offspring:mother		
Fatty acid	Hooded seal pup (prior to suckling):mother[a]	White whale (< 1 week old):mothers[b]	Large living right whale calves (> 6m):mothers[c]
14:0	1.5	1.8	1
16:0	1.5	1.6	1.1
14:1n-5	26	4	0.7
16:1n-7	2.6	2	1
18:1n-9	1.4	0.6	1
20:1n-5	0.5	0.6	1.8
Total Saturated	1.4	1.5	1.1
Total PUFA	0.4	0.6	1.1

Modified from: [a]Iverson et al. 1995, [a]Birkeland et al. 2005, [c]this study.

Table 2.4. Fatty acid composition in potential whale prey (Calanoid copepods and euphausiids). Abbreviations: *Sex and maturity stage*: immature “copepodite” stages of copepods (CV and CVI); juveniles (Juv.); adults (A.); female adults (Fem A.); female subadults (Fem S.); male adults (Male A.); male subadults (Male S.); Fur III (krill furcilia larvae); NA: not applicable. *Location*: Antarctic (Ant.); Lazarev Sea (L S.); Polar Front (P F.); Scotia Sea (S S.); South Georgia (S G.), Weddell Sea (W S.). *Ref.*: references.

Species	**C14:0**	**C16:0**	**C16:1 -n7**	**C18:0**	**C18:1 -n9**	**C18:1 -n7**	**C20:1 -n9**	**C20:5 -n3**	**C22:1 -n11**	**C22:6 -n3**	**Sex and maturity stage**	**Loca-tion**	**Ref.**
Copepods													
C. acutus	4.4	4.5	7.7	0.1	4.8	1.5	23.1	17.1	9.8	11.8	NA	Ant.	a
C. acutus	2.8	3.1	5.2	NA	4	1.3	21.6	19.2	9.2	11.1	CV	W S.	b
C. acutus	5.2	4.6	8.2	NA	4.3	1.5	23.7	19.4	10	12.3	CV	W S.	b
C. acutus	3.6	3.2	8.5	NA	5	1	17.9	20.1	9.4	10.1	Fem A.	W S.	b
C. acutus	4.9	3.8	8.3	0.3	5.9	1.4	27.7	14.9	10.4	8.2	Fem A.	W S.	b
C. acutus	1.9	8	7.6	13.3	5	1.1	20	11.7	9.7	5.6	NA	S S.	c
C. acutus	2.4	2.4	7.7	2.9	4.5	1.1	25.1	16.9	10.5	5	NA	S S.	c
C. propinquus	3.1	11.8	3.5	1.2	2.5	1	2.4	12.6	16.1	9.5	CVI	W S.	d
C. propinquus	3.6	13	4.3	1.3	2.9	1.1	2.7	12.4	20.1	10.9	NA	Ant.	a
C. propinquus	3.5	13	4.2	1.3	2.8	1.1	2.7	13.9	17.7	10.5	CV	W S.	b
C. propinquus	3.4	13.5	5.3	1.3	2.6	0.9	2.7	8.3	25.2	7.3	CV	W S.	b
C. propinquus	3.6	12.2	3.4	1.3	3.1	1	2.9	12.4	19.9	9.6	Fem A.	W S.	b
C. propinquus	3.6	12.3	5.1	1.2	2.6	0.8	2.9	7.6	27.9	7.3	Fem A.	W S.	b
C. simillimus	2.1	11.8	5.1	1.3	1.5	0.9	1	13.3	20.2	6.1	CV	W S.	d
M. gerlachei	4.4	12.3	5.6	1.4	12.8	3.4	1.3	20.9	0.7	24.1	NA	Ant.	a
P. antarctica	1.6	2.4	20.3	0.4	37.9	1.3	2.2	10.5	0.4	12.8	NA	Ant.	a
P. antarctica	0	3	19	NA	24	1	1	14	3	20	CV	P F.	e
P. antarctica	0	2	28	NA	30	1	3	9	3	10	Fem A.	P F.	e
P. antarctica	0	2	28	NA	32	1	2	10	1	11	Male A.	P F.	e

Table 2.4. Continued

Species	**C14:0**	**C16:0**	**C16:1 -n7**	**C18:0**	**C18:1 -n9**	**C18:1 -n7**	**C20:1 -n9**	**C20:5 -n3**	**C22:1 -n11**	**C22:6 -n3**	**Sex and maturity stage**	**Loca-tion**	**Ref.**
R. gigas	0.7	3.3	11.6	0.3	18.2	3.3	0.6	27.4	0.8	15.5	NA	Ant.	a
Euphausiids													
E. superba	11.9	19.3	6.6	1.7	11.7	6.5	1.1	15.2	0.7	8.2	Juv.	L S.	f
E. superba	11.2	24.7	10.2	0.7	12.8	7	1.2	14.8	1.1	6.4	Fem S.	S G.	g
E. superba	11.6	24.6	11.0	1.4	12.5	6.6	1.2	16.1	1.0	6.4	Male S.	S G.	h
E. superba	12.6	24	10.2	1.4	13.4	6.9	1.3	16	1	5.9	Male S.	S G.	h
E. superba	12.2	24	11.2	1.3	13.7	7	1.4	14.9	1.1	6	Fem S.	S G.	h
E. superba	9.5	22.2	8.4	1.6	10.1	7.1	1.2	21.4	0.8	8.8	Male A.	S G.	h
E. superba	9	22.3	8.6	1.3	12.3	7.8	1.1	18.6	0.7	9.2	Fem A.	S G.	h
E. superba	10.8	23.9	9.2	1.2	11.2	7.2	0.8	16.7	0.5	8.8	Juv.	S S.	i
E. superba	10.8	23.4	8.8	1.3	13.2	7	1.2	17	1	7.9	Male S.	S S.	i
E. superba	6.2	21.8	5.3	0.6	8.8	10	0.5	19.6	0.2	15.1	Fem A.	S S.	i
E. superba	12.5	18.2	8.1	1.4	12.8	7.1	1.4	15.3	1	9.1	A.	L S.	f
E. superba	6.7	22.5	7	1.1	11.6	8.9	0.9	18.9	0.4	12.4	Fem A.	S S.	i
E. superba	5	21.6	4.4	1.2	9.4	7	0.5	22.2	0.1	17.5	Male S.	S S.	i
E. superba	3.4	18.7	3.5	1.1	6	5.9	0.9	26.4	0.5	17	Fur. III	L S.	j
E. superba	9.7	24.9	10	0.9	11.7	7	1.1	16.2	0.9	7.5	Juv.	S G.	g
E. superba	10.6	24.8	10	0.7	13.2	6.3	1.2	15.1	0.8	7.1	Male S.	S G.	g
E. superba	9.8	24.4	10.5	0.7	11.5	7.2	1	14.9	0.6	8.3	Fem and male S.	S G.	g

Modified from: Dalsgaard et al. 2003 (a); Hagen et al. 1993 (b); Pond et al. 2012 (c); Kattner et al. 2012 (d); Laakmann et al. 2009 (e); Atkinson & Meyer 2002 (f); Pond et al. 2005 (g); Schmidt et al. 2006 (h); Schmidt et al. 2012 (i); Meyer et al. 2002 (j). See references at the end of this chapter for full citations.

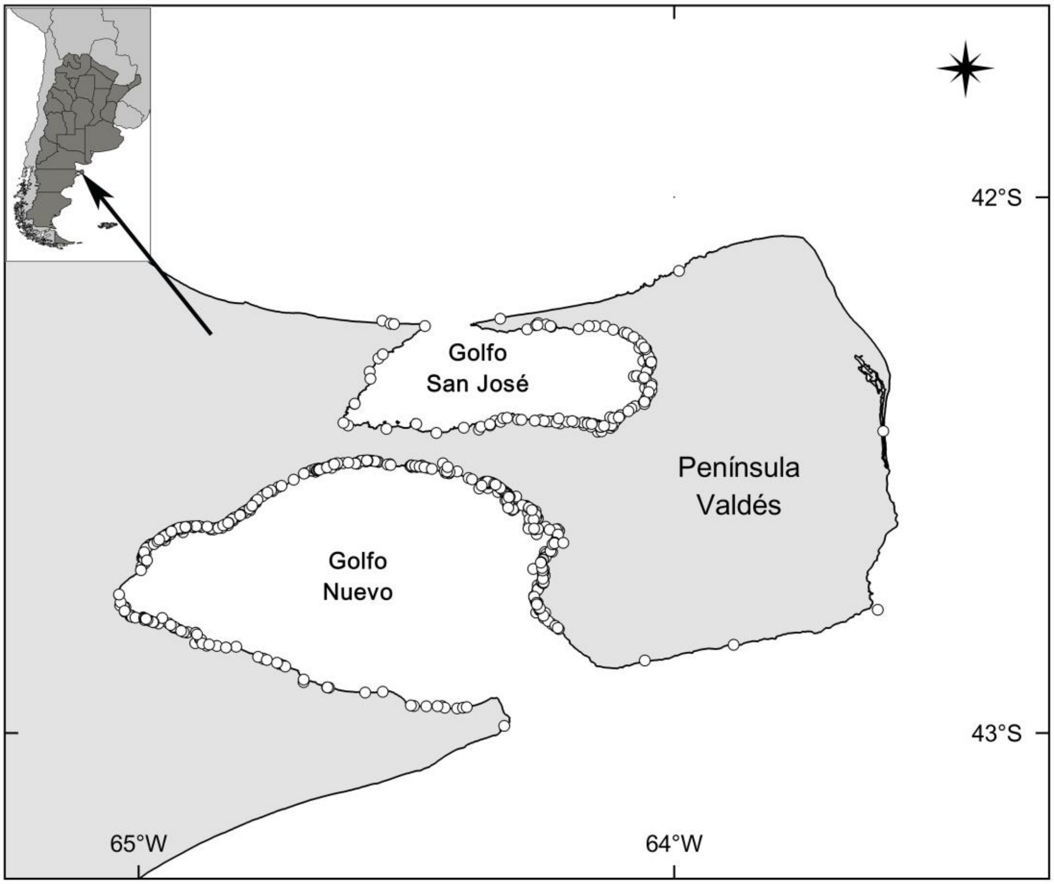

Fig. 2.1. Location of Golfo Nuevo and Golfo San José at Península Valdés, Argentina. White circles represent the locations of 626 dead calves that were found at Valdés in the period 2003-2014.

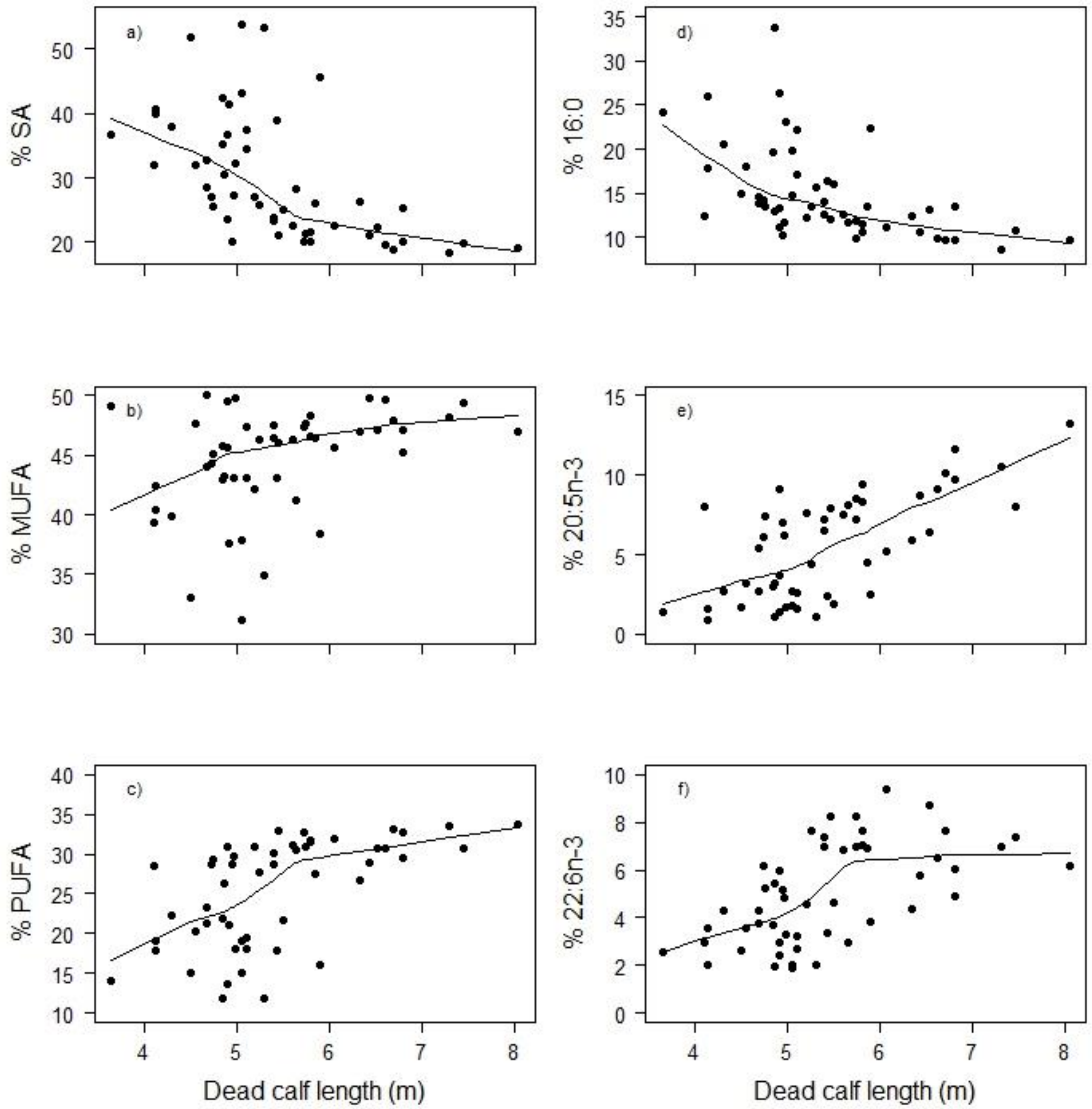

Fig. 2.2. Changes in percent of different fatty acids in the blubber of dead southern right whale calves with body length. Total saturated fatty acids (SA, a) and the saturated fatty acid 16:0 (d) decrease with calf length. Total monounsaturated fatty acids (MUFA, b), total polyunsaturated fatty acids (PUFA, c), and the PUFA 20:5n-3 (e) and 22:6n-3 (f) increase with calf length. Length measurements were taken as a straight line from snout-tip to fluke notch. Note the different scale for the y axis in all the parts (a-e).

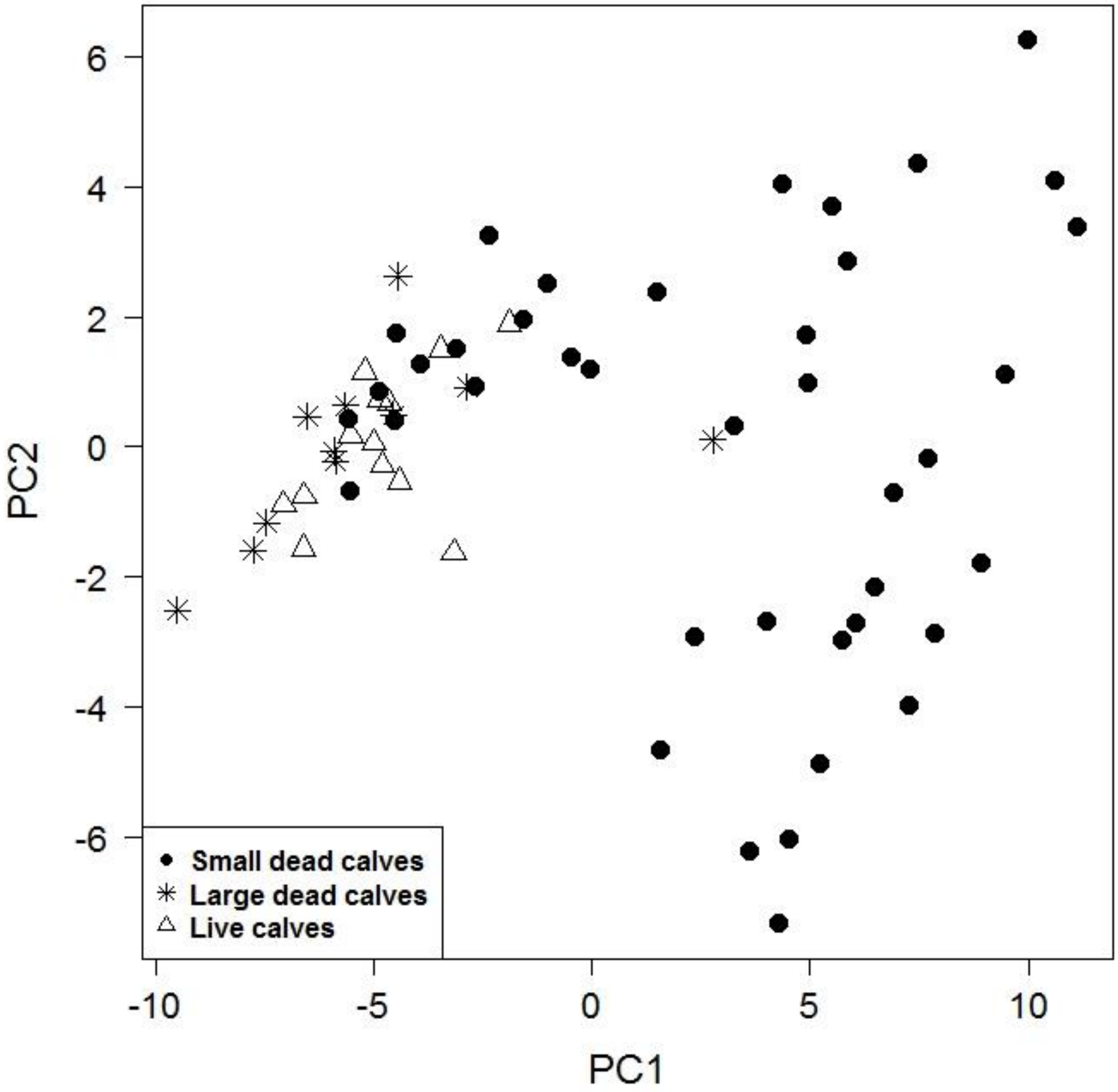

Fig. 2.3. Plot of scores of PC1 and PC2 representing the influence of length on fatty acid composition of dead calves. Large dead calves and living calves (approximately > 6 m in length) are clearly clustered together, while small dead calves (< 6 m) are more dispersed.

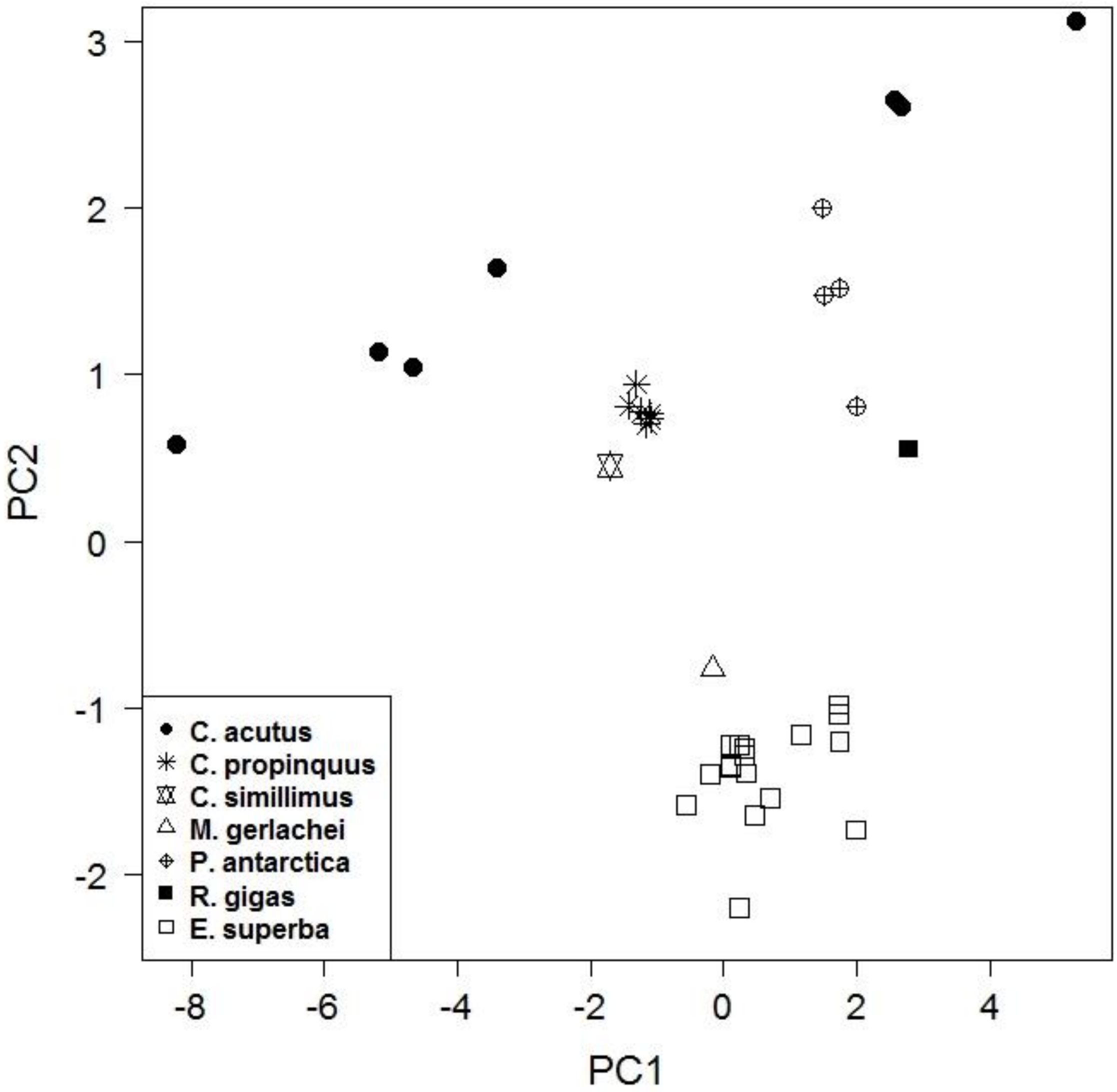

Fig. 2.4. Plot of scores of PC1 and PC2 derived from the analysis of fatty acid composition in whale potential prey. *Calanus propinquus* and *Calanus simillimus* are clustered together and also closer to *Calanoides acutus*. *Euphausia superba* is clustered close to *Metridia gerlachei*, and *Rhincalanus gigas* is closer to *Pareuchaeta antarctica*.

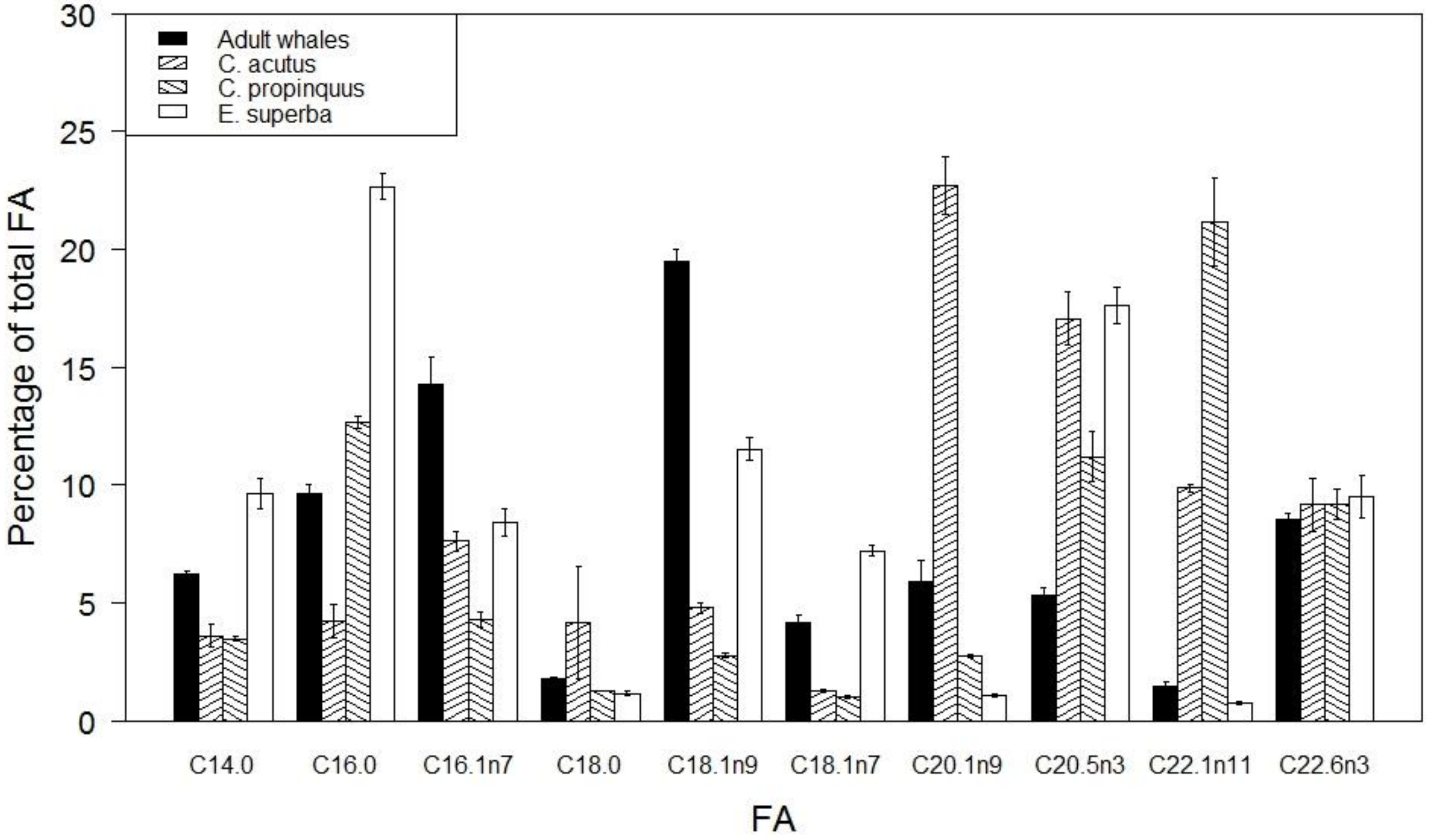

Fig. 2.5. Comparison of relative differences of fatty acid composition between whales and their potential prey (mean ± SE).

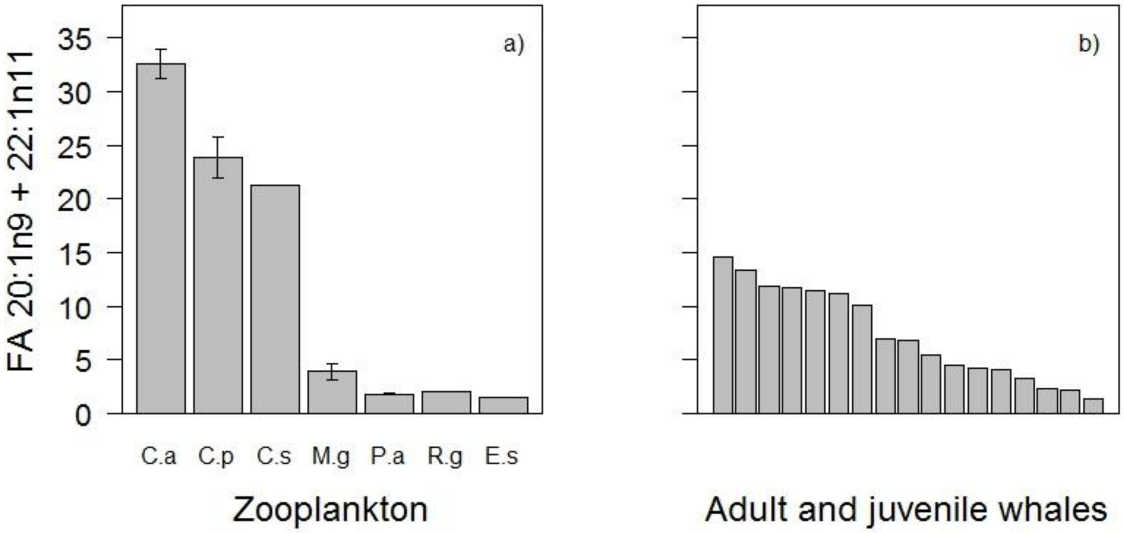

Fig. 2.6. Comparison of the biomarkers of calanoid copepods (20:1n-9 and 22:1n-11) in potential prey (a) and the whales (b). Samples were collected from right whale mothers (*n*=14), adults (*n*=2), and a juvenile (*n*=1). Abbreviations: *Calanoides acutus* (C.a), *Calanus propinquus* (C.p), *Calanus simillimus* (C.s), *Metridia gerlachei* (M.g), *Paraeuchaeta antarctica* (P.a), *Rhincalanus gigas* (R.g), and *Euphausia superba* (E.s).

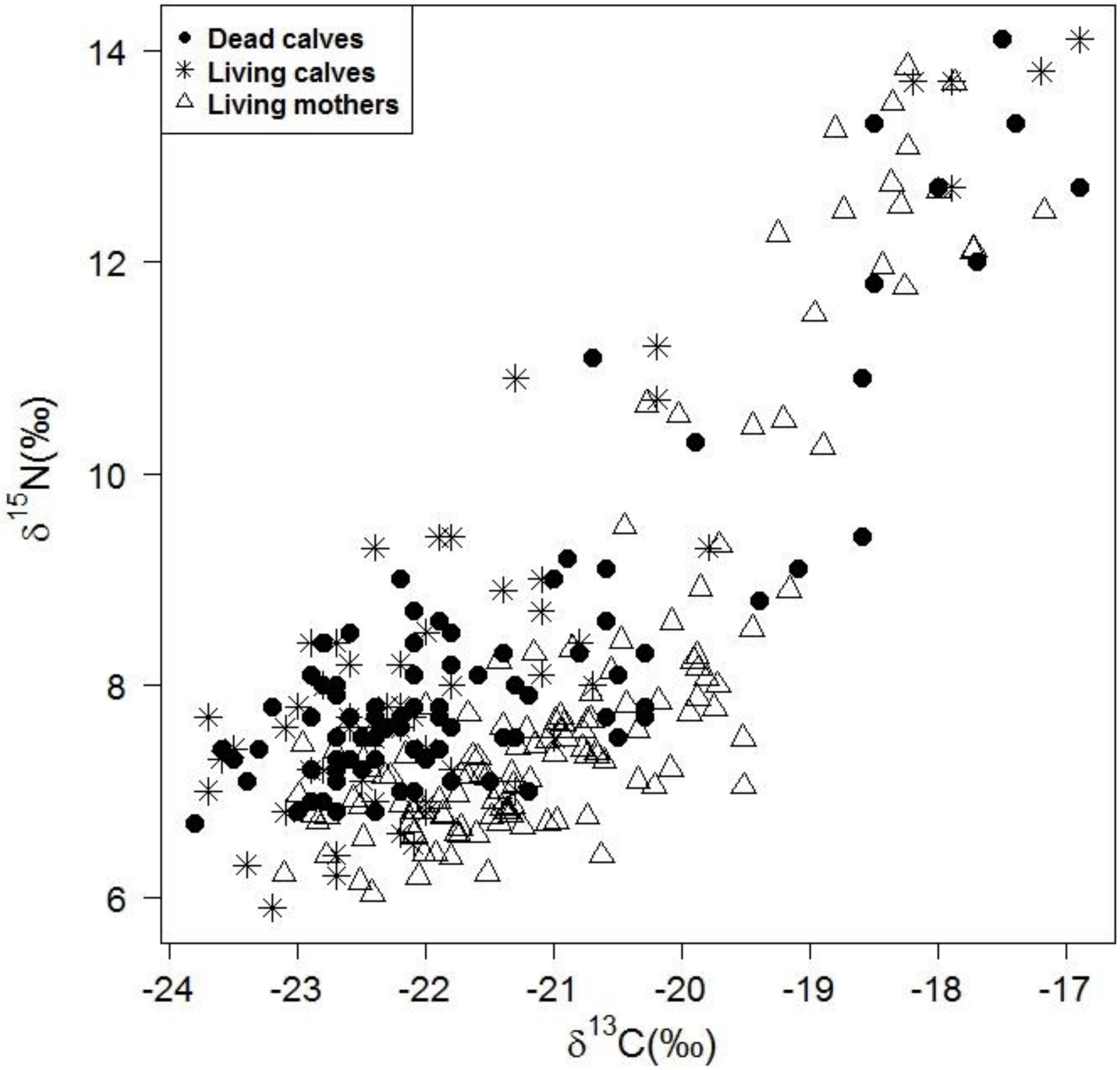

Fig. 2.7. Stable carbon and nitrogen isotope values in the skin of southern right whale living (*n*=89) and dead calves (*n*=58). Statistical analyses indicate no significant differences among these two groups. Isotopic values of 131 living mothers discovered by Valenzuela et al. (2009) were included for visual comparison.

CHAPTER 3

NO EVIDENCE OF MALNUTRITION IN DEAD SOUTHERN RIGHT WHALE CALVES OFF ARGENTINA AS INFERRED FROM BLUBBER THICKNESS MEASUREMENTS

Abstract

Marine mammals rely on their fat layer or blubber to store energy, insulate their bodies and provide buoyancy. Right whale calves are born with a thin blubber layer and need maternal milk to increase lipid reserves and grow. From 2003 to 2014, at least 626 southern right whale (*Eubalaena australis*) calves died at Península Valdés (Argentina) calving ground. Malnutrition has been considered as a possible contributor to these deaths, although anatomical signs of starvation were not evident during necropsies of dead calves. Here, we measured calf length and blubber thickness in nine body locations of 307 dead calves in different states of decay to determine whether their blubber was thinner in high calf mortality (2003, 2005, 2007-2013) compared to years with low calf mortality (2004, 2006 and 2014). We also analyzed whether blubber thickness change with calf growth along the dorsal, lateral and ventral planes, and asked whether it is affected by the intensity of gull-attack lesions. Contrary to what we expected, and controlling for calf length and state of decay, blubber was thinner overall in low mortality years than in high mortality years. Blubber was thicker in longer (older) calves at all body

locations. Along the cranio-caudal axis, dorsal and ventral blubber increased, while lateral blubber decreased towards the peduncle, possibly to streamline the whale's body as occurs in other cetaceans. Blubber thickness was not affected by gull-inflicted lesions. These findings do not suggest a decline in the body fat condition of calves and thus reduced transfer of maternal fat reserves to calves in high mortality years. This is the first study to describe gradual changes in dorsal, lateral and ventral blubber thickness in right whale calves during their first weeks of life.

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 storage of fat reserves in marine mammals and also provides insulation, buoyancy and streamlining (Parry 1949, Pond 1978, Lockyer 1984, Ryg et al. 1988, Kvadsheim et al. 1996, Kvadsheim & Folkow 1997, Toedt 2001, Struntz & McLellan 2004, Berta et al. 2006, Reeb et al. 2007, 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 2014, at least 626 southern right whale (*Eubalaena australis*) calves died at the Península Valdés calving ground, Argentina, from some, as yet, unidentified cause(s) (Uhart et al. 2009, International Whaling Commision [IWC] 2011, Thomas et al. 2013, Rowntree et al. 2013). Poor nutritional state of mothers has been proposed as a potential contributor to these calf deaths (IWC 2011, Thomas et al. 2013).

The reproductive success of the Valdés southern right whale population has been correlated with the abundance of one of their main prey, Antarctic krill (*Euphausia superba*); thus, when the abundance of krill declines after El Niño events, females have fewer calves than expected (Leaper et al. 2006). A reduction in diet quality or quantity is likely to affect milk yield in whale mothers, affecting their calves' body condition and/or survival, as has been demonstrated in other mammals (Oftedal 1985, Ono et al. 1987, Iverson et al. 1991). In the California sea lion, a reduction of food availability during the 1983-84 El Niño was linked to a decrease in milk production and under-development of their suckling offspring (Iverson et al. 1991). Southern right whale calves feed exclusively on milk during the three to four month period at the Valdés calving ground (Taber & Thomas 1982, Thomas & Taber 1984). Evidence of reduced maternal body condition has been shown during some years with high calf mortality at Valdés. Rowntree measured the blow intervals of mother-calf pairs at Valdés in 1997, 2004-06 and 2008-09 (Sironi & Rowntree 2013), assuming that longer breathing intervals would reflect a better body condition of whales as has been shown in humans (Ofir et al. 2007) and suggested in humpback whales (*Megaptera novaeangliae*) (Chu 1988). Right whale mothers breathed at shorter intervals in 2008 and 2009 (when the majority of dead stranded calves were smaller in size) suggesting that mothers were in worse body condition than mothers in 2005 (when most dead calves were larger) (IWC 2011). Although there is insufficient information on maternal body condition of right whales at Valdés, blubber thickness measurements have been taken continuously since 2003 (the beginning of the high calf mortality events) from a large number of dead calves offering an opportunity to assess their body condition, and indirectly that of their mothers, through time.

Blubber thickness of calves could be also affected by the presence and number of gull-inflicted lesion on their backs. Wounding is caused by Kelp Gull (*Larus dominicanus*) harassment on southern right whales, which has been observed since the 1970s at Península Valdés and has increased considerably in the 2000s (Cummings et al. 1972, Thomas 1988, Rowntree et al. 1998, Sironi et al. 2009, Fazio et al. 2012). Gull harassment negatively affects the behavior, energy expenditure and probably the body condition of mothers and their calves. Mother-calf pairs harassed by gulls reduce by 25% the time spent in low-energy activities (e.g., resting and traveling slowly) (Rowntree et al. 1998). Low-energy activities are the predominant behaviors of lactating right whale mothers at Valdés when not disturbed by gulls (Thomas & Taber 1984, Thomas 1988, Rowntree et al. 1998). Lactating mothers are fasting at Valdés and rely on blubber reserves for self-maintenance and nursing throughout the calving season. Calves may not be able to accumulate enough blubber if mothers and calves invest more energy and time fleeing Kelp Gulls than resting and nursing.

Blubber thickness can be used as an indicator of body fat condition in dead and living cetaceans (Lockyer 1986, 2007, Koopman et al. 2002, Gulland & Hall 2005, Miller et al. 2011, 2012, Bradford et al. 2012). Ultrasound measurements of blubber thickness of living southern right whale calves indicate that their body fat condition improves during the first months of life at their calving ground (Miller et al. 2011, 2012), likely essential for energy reserves, buoyancy and thermoregulation. Blubber is not homogeneously distributed throughout the body of cetaceans. The posterior (caudal) region of the body seems to represent an important fat storage area in baleen whales with the thickest blubber layers recorded at the dorsal- and ventral-posterior regions (Slijper 1948, Lockyer et al. 1985, Lockyer & Waters 1986, Næss et al. 1998). The posterior-lateral blubber, however, tends to decrease when reaching the caudal region, possibly to help streamlining the whale's body (Lockyer 1984, Lockyer & Waters 1986, Næss et al. 1998, Reeb et al. 2007).

Detailed information on body fat condition in right whale calves is lacking. Blubber thickness measurements at the lateral-anal site were recorded during whaling expeditions conducted mainly at the Southwest Atlantic ocean in the 1960s, but most harvested right whales were juveniles and adults (larger than 8 m) (Tormosov et al. 1998). Ruler blubber measurements have been reported for five dead right whale calves off South Africa, yet all these individuals were very small (<6 m in length) (Reeb et al. 2007). Acoustic measurements of blubber thickness have been published for living southern right whale calves off South Africa and for North Atlantic right whale calves *E. glacialis* (Miller et al. 2011, 2012). However all measurements were from the dorsum as they were taken from animals in the water. Blubber thickness measurements of the southern right whales breeding at Península Valdés in Argentina are not yet available. The recent right whale mortality events at Península Valdés provide an opportunity to study basic aspects of blubber thickness at numerous body sites along the dorsal, lateral and ventral axes of the calf's body, in a large number of animals, and allows for a detailed evaluation of how blubber thickness changes in calves of different length or age.

Here, we compared blubber thickness in different body locations (dorsally, ventrally and laterally along the axillary, umbilical and anal girths) in calves that died in the period 2003-2014 to study changes in blubber thickness during calf growth. We included data about dead juveniles and adults to extend our understanding of changes in blubber thickness in later life stages. We also evaluated if blubber was consistently thicker in years of low calf mortality than in years with high calf mortality. Additionally, we determined whether blubber thickness was affected by state of decomposition, sex and stranding location at Península Valdés (Golfo Nuevo vs. Golfo San José). Finally, we evaluated whether blubber was thicker on calves with gull-inflicted lesion on their backs.

Materials and Methods

Necropsies

Necropsies of southern right whale calves, juveniles and adults were conducted from June to December at Península Valdés (Golfo Nuevo and Golfo San José) in the period 2003-2014 by the Southern Right Whale Health Monitoring Program (SRWHMP). The SRWHMP team recorded blubber thickness, total length, carcass decomposition and sex of individuals, along with date of necropsy and location. Most stranded animals were calves (3 to 9 m in length) from newborns to calves less than four months old (Uhart et al. 2008, 2009, Sironi et al. 2014). Because the majority of calves are born in August at an average length of 5.5 m (Whitehead & Payne 1981), dead calves were often shorter than 6 m if stranded early in the season (before 1 October) and longer than 6 m if stranded late in the season (on or after 1 October) (Rowntree et al. 2013).

Blubber Thickness and Length Measurements

Blubber thickness was determined *in situ* at three body girths in dead calves, juveniles and adults when their stranded position and state of decay allowed it. 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. 3.1). 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 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. 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).

Body length from snout-tip to fluke notch, measured in meters with a measuring tape, was also recorded in calves, juveniles and adults. All length measurements were taken in a straight line (not following the curve of the body) independently of the whale's stranding position. 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).

Carcass Decomposition

A necropsy carcass condition code was assigned to each whale based on the state of decomposition of tissues and organs (Uhart et al. 2009). For this study, we selected only dead calves in conditions 2, 3 and 4 (Geraci & Lounsbury 2005). Samples were not collected from calves in condition code 5 (dry carcass with pieces of skin and bones).

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, absence protrusion of tongue and penis and internal organs conserved. Condition code 3 included dead calves with an intact carcass but bloated, mild odor, wrinkled and detached skin, possible scavenger damage, sunken or missing eyes, dry mucous membranes, tongue and penis protrusion and most internal organs conserved. Condition code 4 included dead calves with an intact carcass but internally collapsed, strong odor, detached skin, severe scavenger damage, easy detachment of fat and muscle tissues and most internal organs liquefied (Geraci & Lounsbury 2005). In this study, all blubber thickness comparisons were adjusted for necropsy carcass condition (see Statistical Analyses).

Stranding Time in the Season

To analyze how body fat condition of calves changes through the season, we compared blubber thickness at the nine body locations in calves that died early in the season (before 1 October) and calves that died late in the season (on or after 1 October). Calves that died early in the season were mainly newborns, while calves that died late in the season were generally older (larger) (Rowntree et al. 2013).

High and Low Mortality Years

We defined “high mortality” and “low mortality” years in the 2000s to evaluate whether the blubber thickness of calves decreased in high calf-mortality years when causes of calf death might be related to malnutrition. In low mortality years, the number of dead calves was not significantly greater than expected (2004, 2006 and 2014), and in high mortality years, the number of dead calves was significantly greater than expected (2003, 2005 and 2007-2014) (see Chapter 5).

Gull-Inflicted Lesions

To evaluate whether blubber thickness of calves was associated to gull-inflicted lesions (i.e., calves with more lesions have thinner blubber), we recorded the presence and number of lesions on calves that died in 2003-2011 (note that for all the other analyses conducted in this study, we used data collected during the period 2003-2014). Briefly, the presence of lesions was determined categorizing each dead calf into two possibilities: “yes” if the calf had at least one lesion or “no” if it had no lesions. Number of lesions was assigned as zero for calves with zero lesions (“n”) and one or more for calves with lesions (“y”). For a detailed description of this methodology, see Chapter 4. In this study, we categorized each calf according to the number of lesions counted, as follows: calves without lesions, calves with 1 to 5 lesions, calves with 6 to 10 lesions, calves with more than 10 lesions.

Statistical Analyses

Linear regression models were used on each of the nine blubber measurements to determine how blubber thickness changes with calf length. Adjusting by length, we ran linear models to evaluate whether blubber thickness varies with necropsy condition (all models were run with and without interaction between length and necropsy condition). Linear models were also used to evaluate differences in blubber thickness of dead calves in relation to the following independent variables: a) stranding time in the season (early or late), b) low and high mortality years, c) location (Golfo Nuevo and Golfo San José), d) calf sex, e) presence or absence of gull-inflicted lesions on the calf's back, and f) number of gull lesions (four categories assigned, factor variable). All these models were adjusted for calf length and necropsy carcass condition (covariates). Models used to evaluate whether gull-inflicted lesions affect the thickness of the blubber were run with and without interaction. Blubber thickness of juveniles and adults was included in this study only to serve as a reference for comparison to the blubber thickness of calves. Statistical analyses were not conducted for these two groups due to their small sample size (11 juveniles and 9 adults). To determine changes in the patterns of fattening with growth along the cranio-caudal axis of the calf's body, we compared blubber thickness at the dorsal, lateral and ventral regions among calves of different lengths. All statistical analyses were conducted using R software version 3.1.1 (R Core Team 2013).

Results

Blubber Thickness Increases with Calf Length

Both length and at least one blubber thickness measurement were recorded in 307 calves that died at Península Valdés from 2003 to 2014. 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, $0.45 \leq R^2 \leq 0.62$, all *p*-values < 0.001). The length of calves analyzed for blubber thickness ranged from 3.15 to 8.42 m. Blubber thickness ranged from an average of 3.96 cm at the dorsal-axillary (dorsal-1) site to an average of 9.70 cm at the ventral-anal (ventral-3) site (Table 3.1, Fig.

3.1). The minimum and maximum calf blubber thicknesses recorded 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). Blubber thickness was greater in juveniles (*n*=11) and adults (*n*=9) (Table 3.1).

Blubber Thickness Often Does Not Change with Carcass Decay

Controlling for calf length, carcass decomposition status had no detectable effect on seven blubber thickness measurements among calves of similar size (regression, *p*-values ranged from 0.23 to 0.78). However, blubber thickness at the dorsal-1 (ANOVA, $p = 0.02$) and lateral-1 sites (ANOVA, $p = 0.003$) varied among calves in condition codes 4 and 3. In consequence, the analyses described below were adjusted *in all cases* by calf length and state of decay.

Blubber Thickness Differs Between Stranding Locations but Not Between Sexes

Calves that died in Golfo Nuevo had thinner blubber than those dying in Golfo San José in eight out of nine blubber thickness measurement sites. From these eight measurements, only five were significantly different (regression, *p*-values ranged from 0.002 to 0.05) and three were not (regression, dorsal-axillary $p = 0.28$, dorsal-umbilical $p = 0.84$, ventral-3 $p = 0.06$). Calves that died in Golfo Nuevo had thicker blubber than calves that died in Golfo San José only at the dorsal-3 site, but this difference was not significant (regression, $p = 0.35$).

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*-values ranged from 0.07 to 0.84).

Calves that Died Late in the Season Have Thicker Blubber

Blubber was overall thicker in calves that died at Valdés late in the season (on or after 1 October, *n*=223) compared to calves that died early in the season (before 1 October, *n*=84), but this difference was significant only at the dorsal-1 (regression, p = 0.05) and dorsal-2 sites (regression, p = 0.02, Table 3.1).

Calves that Died in High Mortality Years Have Thicker Blubber

Blubber was thicker in calves that died in high mortality years at eight out of nine blubber sites compared to low mortality years, but this difference was significant only at the dorsal-1 (regression, p = 0.04), lateral-1 (regression, p = 0.03) and lateral-2 sites (regression, p = 0.05) (Table 3.2). More calves that died in high mortality years were large (*n*=117, 41%) compared to low mortality years (*n*=7, 32%) (Table 3.2). Calf blubber was thinner in high mortality years only at the dorsal-3 site but this difference was not significant (regression, p = 0.6, Table 3.2).

Gull-Inflicted Lesions Appear Not to Affect Blubber Thickness

Blubber was thinner in calves without lesions than in calves with lesions (Fig. 3.2a and 3.2b) in all blubber thickness measurements (regression models with and without interaction, all p values ≤ 0.05, Table 3.3). However, most calves without lesions were smaller than 6 m.

Blubber was thinner in calves with zero lesions compared to calves with more than 10 lesions in the lateral-1, -2, -3 sites (regression, all *p* values ≤ 0.007, *p* = 0.08 for lateral-2 model with interaction, Table 3.3). Number of lesions had no detectable effect in the other six blubber measurement sites (regression, all *p*-values ranged from 0.16 to 0.93). Most calves with zero lesions were small calves (Fig. 3.3a and 3.3b).

Calves Acquire a Streamlined Body Shape with Growth

Along the cranio-caudal axis, blubber thickness of calves of increasing lengths augmented dorsally and ventrally (Fig. 3.1, Fig. 3.4). Blubber at the dorsal-1 site was thinner than the other two more caudal dorsal sites, but this difference was only significant for dorsal-1 vs. dorsal-3 comparison (regression, *p* = 0.01). Similarly, blubber at the ventral-1 site was thinner than the other two more caudal ventral sites, but this difference was not significant. Laterally, blubber was thicker at the lateral-2 site (center) than at the lateral-1 (close to the head) and lateral-3 (close to the peduncle) sites, but this difference was significant only for lateral-2 vs. lateral-3 (regression, *p* = 0.02).

On the axillary and umbilical girths, the increase in blubber thickness with calf length was greater on the ventral surface (Fig. 3.4). Blubber at the dorsal-1 site was thinner than blubber at the lateral-1 and ventral-1 sites, but this difference was only significant for the dorsal-1 vs. lateral-1 comparison (regression, *p* = 0.006). Similarly, blubber at the dorsal-2 site was thinner than blubber at the lateral-2 and ventral-2 sites, but in this case both differences were significant (regression, dorsal-2 vs. lateral-2 comparison: *p* = 0.01, dorsal-2 vs. ventral-2 comparison: *p* = 0.007). For the most caudal girth, the anal girth, blubber was thinner at the lateral-3 site than at the upper dorsal and lower ventral sites, but these differences were not significant in any case.

Discussion

As expected, we found that blubber thickness increased with calf growth, yet these variations differed by location in the calf's body, suggesting a selective pattern in fat deposition. We failed to find differences in calf blubber thickness that could associate high mortality years with a direct nutritional factor affecting blubber fat storage. This implies that mechanisms other than limiting accumulation of fat reserves might have played a role in recent calf die-off events. Blubber thickness was not apparently affected by gull-inflicted lesions.

Blubber thickness increases with growth in cetaceans (Lockyer 1991, Struntz & McLellan 2004, Miller et al. 2011, 2012). We found similar results for southern right whale calves at Península Valdés. Dead calves examined here ranged from neonates (<6 m) to calves up to 8.42m. 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 blubber thickness with body length was not found in living North Atlantic right whale calves (*E. glacialis*) (Miller et al. 2011), but this result may differ with findings in southern right whales because only a small number of *E. glacialis* calves (*n*=9) could be measured within a limited range of lengths (~8.5 to 10 m). Blubber thickness increases as well in southern right whale juveniles and adults harvested during illegal whale catches in the 1960s (Tormosov et al. 1998) and in living North Atlantic right whale juveniles (Miller et al. 2011).

Patterns of blubber distribution over the calf's body change with growth. We found that dorsal and ventral blubber thickens towards the caudal region of the body, while lateral blubber diminishes towards the tail. A similar pattern of fattening was found by Reeb et al. (2007) in five southern right whale calves off South Africa. Our results support previous studies showing the role of blubber as a structural tissue that laterally streamlines the body of whales (Slijper 1948, Lockyer et al. 1985, Lockyer & Waters 1986, Næss et al. 1998) and thus improves propulsion (Pabst et al. 1999, Summers 2001, Hamilton et al. 2004). We also found that blubber thickness increases 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 is 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 did not change with carcass decomposition except for two blubber measurement sites taken dorsally and laterally along the axillary girth. Most calves found dead at Valdés are in advanced state of decay (condition code 4 or 5) because an unknown period of time (rarely hours but mostly days or weeks) occurs between their deaths and their necropsy examinations (Uhart et al. 2008, 2009). 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 acurostrata*) did not seem to vary when comparing samples taken 24 hours after death to samples taken one month after death, but lipid content of blubber, which seems more sensitive to degradation (Borrell & Aguilar 1990, Gulland & Hall 2005), decreased significantly during that same period of time. Our findings suggest that blubber thickness measurements may not be affected as much by the state of decay of the whale, at least for calves in conditions 2 to 4.

Sex had no detectable effect on 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. These females had the thickest blubber prior to (Miller et al. 2011) and during pregnancy (Lockyer 1981, 1986, 1987) 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, an expected finding considering that it takes southern right whale calves a long time until they reach the blubber thickness of adults (Table 3.1, Fig. 4 and Fig. 5 in Miller et al. 2011). However, in the harbour porpoise, blubber is thicker in female neonates compared to males, maybe to favor female calf survival (Lockyer 1995).

Blubber tended to be thinner in calves that died earlier in the season compared to calves that died later in the season. Fat reserves are expected to increase with nursing. Acoustic blubber thickness measurements on the living right whales off South Africa indicate that blubber is thinner in early-nursing compared to midnursing ones (Miller et al. 2011). We found that the Valdés calves follow a similar pattern with thinner blubber in young calves that died early in the season, and probably had not spent a long time nursing, and thicker blubber in older calves that died later in the calving season, that may have nursed longer.

Blubber was thinner overall in calves that died in low mortality years compared to calves that died in high mortality years. This unexpected finding can be attributed to differences in sample size in both groups. Measurements collected in low mortality years came from only 22 calves in three separate years, while data for high mortality years were collected from 285 calves in eight different years. The smaller sample size in low mortality years may not provide a realistic picture of the body condition of calves that died in low mortality years. Another plausible explanation for this difference is that calves that died in low mortality years were in worse condition than calves that died in high mortality years. The cause of death of most calves that died either in low or in high mortality years has not yet been identified. Data from the majority of calf necropsies at Valdés do not suggest debilitation or emaciation either in low or high mortality years. Furthermore, fat marrow content in the bones of the dead calves was also normal for their age range (D. McAloose et al. submitted). In baleen whales, emaciation is evident through a reduction in dorsal blubber behind the blowholes that makes the scapulas of whales 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 vast majority of calves. However, it is striking that calves that died in Golfo Nuevo had thinner blubber than those of similar size that died in Golfo San José, as Golfo Nuevo is the location where most calf deaths have been recorded during high mortality years (Uhart et al. 2008, 2009, Rowntree et al. 2013, Sironi et al. 2014) and where Kelp gull attack frequencies tend to be higher (Sironi & Rowntree 2013, see Chapter 4).

Although blubber tended to be thinner in calves without gull-inflicted lesions compared to calves with lesions, most calves without lesions were small (≤6 m) and probably died shortly after birth without time to accumulate lesions (whales accumulate lesions throughout the calving season, Thomas 1988, see Chapter 4). On the other hand, most calves with one or more lesions tended to be larger than 6 m. These findings may indicate that overall gull attacks may not affect calf fattening. However, gull harassment cannot be ruled out as a contributor to calf deaths since gull harassment could be increasing stress levels in mothers and calves and could negatively affect their health through dehydration or loss of thermoregulatory capacity (Thomas et al. 2013).

Although we found no evidence of thinner blubber in calves that died during high mortality years, a nutritional factor cannot be ruled out as a contributor for the calf deaths. Many other analyses, including lipid content in blubber, blubber composition, as well as body girths and size, could provide a more comprehensive picture of overall physical condition (Rice & Wolman 1971, Lockyer et al. 1985, Lockyer 1986, 1993, Caon et al. 2007). The present study did not attempt to compare the body condition of dead and living calves because data are lacking for living calves at Península Valdés. Ongoing behavioral (e.g., blowing intervals in mothers and calves), nutritional (e.g., diet composition of mothers) and physiological (e.g., urine metabolites related to starvation in dead calves) analyses could all supplement the findings presented in this study. To date, no common cause has been found for the calf deaths at Valdés (Rowntree et al. 2013), although Kelp Gull attacks are unique to this right whale calving ground and have drawn much attention as a contributor (Thomas et al. 2013). Ongoing research should continue and new avenues for research should be explored to evaluate the health of the Península

Valdés southern right whale population.

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Table 3.1. Mean and standard deviation of blubber thickness measurements in calves that died early in the calving season (before 1 October), calves that died late in the season (after 1 October), juveniles and adults. 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. * indicates significant *p*-values. Sample size for each group is shown in parentheses. Data were collected during necropsies from 2003 to 2014 at Península Valdés, Argentina.

Measuring site	**Early-season dead calves** (*n*=223) Length: 5.59±0.90			**Late-season dead calves** (*n*=84) Length: 6.30±1.13			**Early vs. late**	**Juveniles** (*n*=11) Length: 11.41±0.78			**Adults** (*n*=9) Length: 14.34±1.45		
	Mean	SD	n	Mean	SD	n	p-value	Mean	SD	n	Mean	SD	n
Dorsal-1	3.96	1.82	162	5.68	3.03	50	*0.05	12.44	2.65	9	20	NA	1
Dorsal-2	4.9	2.26	162	7.11	3.17	48	*0.02	13.1	2.69	9	12	3.46	3
Dorsal-3	7.09	3	162	8.83	3.79	47	0.54	17.23	5.69	9	13.75	1.06	2
Lateral-1	6	2.79	206	7.63	3.77	69	0.84	15.61	3.99	11	18.67	6.03	3
Lateral-2	6.11	2.59	208	8.35	3.57	72	0.11	15.6	3.67	11	19.07	4.44	6
Lateral-3	6.37	2.26	182	7.75	3.49	67	0.82	13.69	2.51	10	16.83	2.48	6
Ventral-1	6.09	2.43	125	7.97	3.06	40	0.69	14.72	3.02	9	20.8	10.41	5
Ventral-2	6.37	2.26	136	8.86	3.60	45	0.32	16.88	4.52	9	18.83	5.78	6
Ventral-3	8.08	2.67	112	9.58	3.59	46	0.76	16.01	3.46	7	18.75	5.35	6

Table 3.2. Mean and standard deviation of blubber thickness measurements in calves that died in low mortality years (2004, 2006 and 2014) and calves that died late in high mortality years (2003, 2005, 2007-2013). 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. At least one blubber thickness measurement was taken in 22 calves that died in low mortality years and 285 calves that died in high mortality years. * indicates significant *p*-values. Data were collected during necropsies from 2003 to 2014 at Península Valdés, Argentina.

Measuring site	**Low mortality years** (2004, 2006 and 2014, *n*=22) Length: 5.66±0.84 m (32% ≥ 6 m)			**High mortality years** (2003, 2005, 2007-2013, *n*=285) Length: 5.79±1.03 m (41% ≥ 6 m)			
	Mean	SD	n	Mean	SD	n	p-value
Dorsal-1	3.40	1.81	15	4.44	2.30	197	*0.04
Dorsal-2	4.51	2.16	15	5.48	2.68	195	0.19
Dorsal-3	7.56	3.29	15	7.48	3.28	194	0.60
Lateral-1	5.20	2.93	22	6.51	3.14	253	*0.03
Lateral-2	5.64	2.82	22	6.77	3.03	258	*0.05
Lateral-3	5.95	2.69	11	6.78	2.71	238	0.38
Ventral-1	6.10	2.84	15	6.59	2.70	150	0.28
Ventral-2	6.17	2.44	15	7.09	3.24	166	0.15
Ventral-3	7.95	3.14	6	8.54	3.04	152	0.75

Table 3.3. Linear models (with interaction and without interaction) of nine blubber thickness measurements in relation to presence of gull-inflicted lesions (calves with lesions and without lesions) and number of lesions. All models were run adjusted by calf length and carcass decomposition condition. * indicates significant *p*-values. 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. Data were collected during necropsies from 2003 to 2011 at Península Valdés, Argentina.

Measuring site	**Presence of lesions**		**Number of lesions**	
	No interaction	Interaction	No interaction	Interaction
Dorsal-1	0.09	< 0.001*	0.21	0.39
Dorsal-2	0.05*	0.08	< 0.001*	< 0.001*
Dorsal-3	0.04*	0.31	0.45	0.63
Lateral-1	0.37	< 0.001*	0.23	0.57
Lateral-2	0.003*	0.003*	0.007*	0.08
Lateral-3	0.08	< 0.001*	0.60	0.41
Ventral-1	0.73	0.01*	0.83	0.80
Ventral-2	0.01*	0.09	0.005*	< 0.001*
Ventral-3	< 0.001*	0.08	0.16	0.93

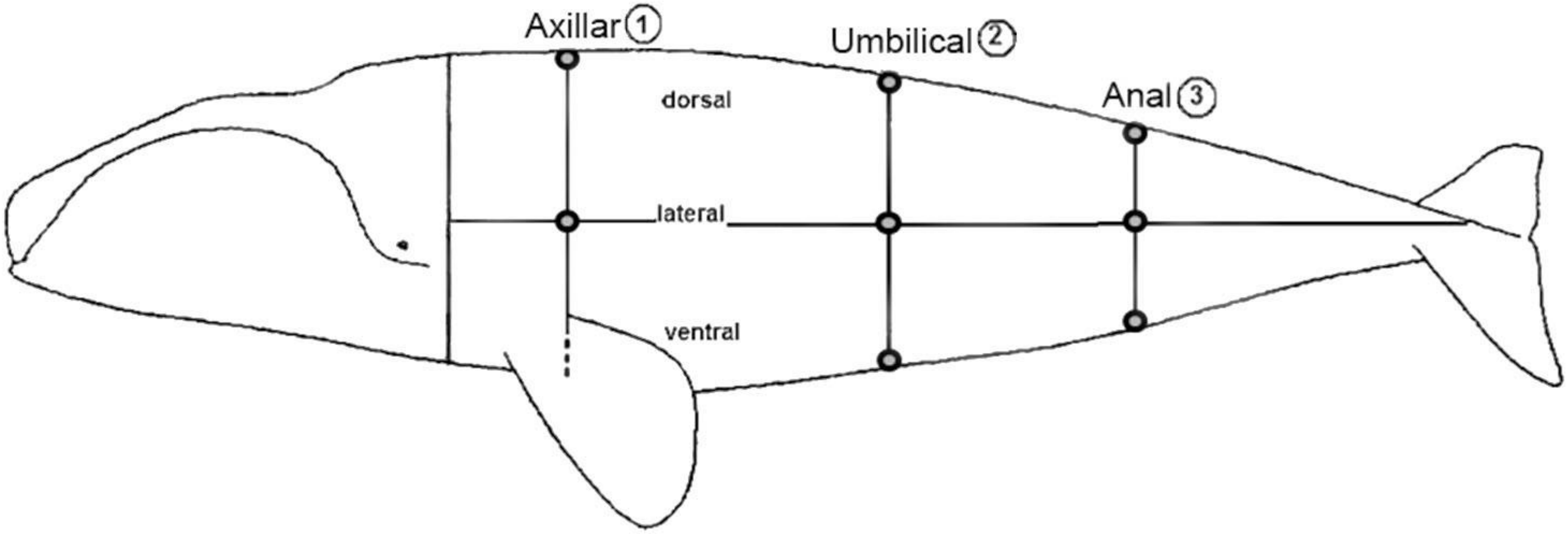

Fig. 3.1. Measuring sites on the body of southern right whales. Blubber thickness was measured following the cranio-caudal axis at the dorsal, lateral and ventral sites along the axillary (-1), umbilical (-2) and anal (-3) girths. (The ventral-axillary measurement is not shown in the drawing).

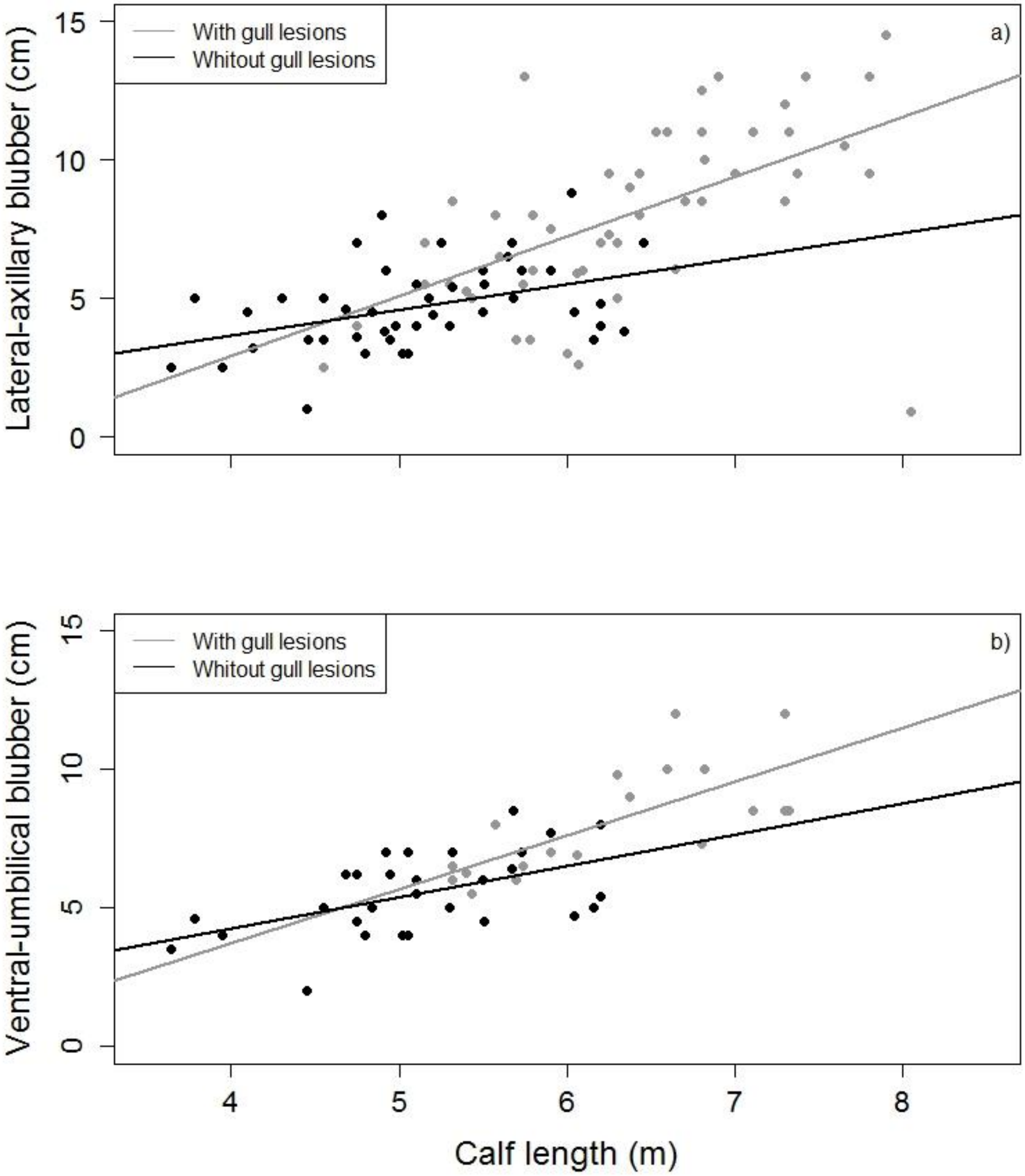

Fig. 3.2. Blubber thickness in relation to length for calves with (grey dots) and without (black dots) lesions. Blubber thickness was taken in centimeters and length in meters. Parts a) and b) illustrate two out of nine blubber measurement locations, the lateral-axillary (a) and ventral-umbilical (b) positions. Data were collected during necropsies from 2003 to 2011 at Península Valdés, Argentina.

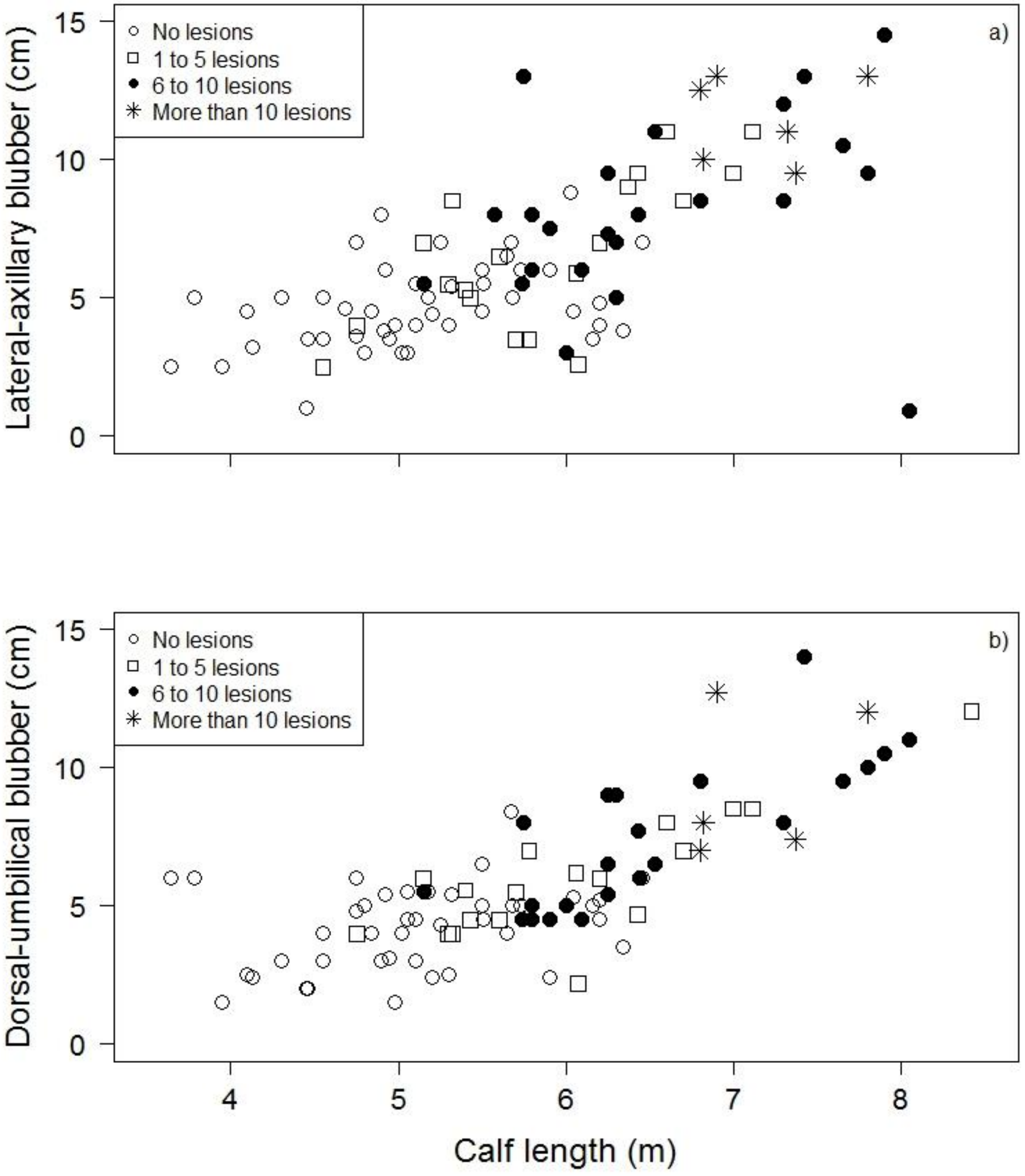

Fig. 3.3. Blubber thickness in relation to length for calves without (open circles), with 1 to 5 (open squares), with 6 to 10 (black circles) and more than 10 gull-inflicted lesions (asteriks). Blubber thickness was taken in centimeters and length in meters. Parts a) and b) illustrate two out of nine blubber measurement locations, the lateral-axillary (a) and dorsal-umbilical (b) positions. Data were collected during necropsies from 2003 to 2011 at Península Valdés, Argentina.

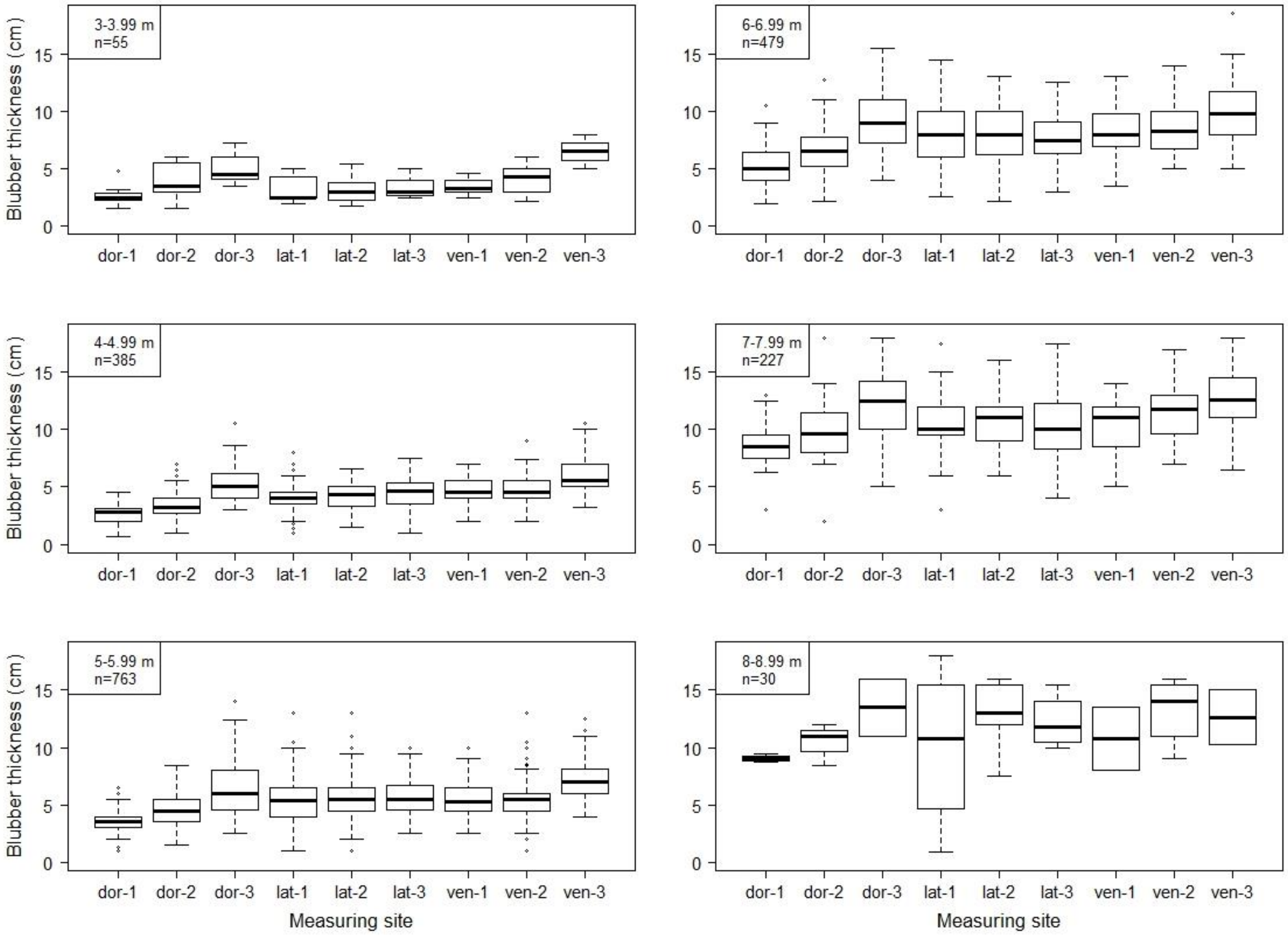

Fig. 3.4. Blubber thickness along nine different sites in the calf's body for calves of different length. Blubber thickness was taken in centimeters. Calf size range (in meters) and sample size (number of blubber measurements taken in total for a specific calf size range) are indicated in each part. Abbreviations: dor-1 (dorsal-axillary), lat-1 (lateral-axillary), ven-1 (ventral-axillary), dor-2 (dorsal-umbilical), lat-2 (lateral-umbilical), ven-2 (ventral-umbilical), dor-3 (dorsal-anal), lat-3 (lateral-anal), ven-3 (ventral-anal).

CHAPTER 4

INCREASED WOUNDING OF SOUTHERN RIGHT WHALE CALVES BY KELP GULLS AT PENÍNSULA VALDÉS

Abstract

At least 626 southern right whale (*Eubalaena australis*) calves died at the Península Valdés calving ground, Argentina, between 2003 and 2014. Intense gull harassment may have contributed to these deaths. In the 1970s, Kelp Gulls (*Larus dominicanus*) began feeding on skin and blubber pecked from the backs of living right whales at Valdés. The frequency of gull attacks has increased dramatically over the last three decades and mother-calf pairs are the primary targets. Pairs attacked by gulls spend less time nursing, resting and playing than pairs not under attack. In successive attacks, gulls open new lesions on the whales' backs or enlarge preexisting ones. Increased wounding could potentially lead to dehydration, impaired thermoregulation, and energy loss to wound healing. The presence, number and total area of gull-inflicted lesions were assessed using aerial survey photographs of living mother-calf pairs in 1974-2011 (*n*=2680) and stranding photographs of dead calves (*n*=192) in 2003-2011. The percentage of living mothers and calves with gull lesions increased from an average of 2% in the 1970s to 99% in the 2000s. In the 1980s and 1990s, mothers and calves had roughly equal numbers of lesions (one to five), but by the 2000s, calves had more lesions

(nine or more) covering a greater area of their backs compared to their mothers. Living mother-calf pairs and dead calves in Golfo Nuevo had more lesions than those in Golfo San José. The number and area of lesions increased with calf age during the calving season. Intensified Kelp Gull harassment at Península Valdés could be compromising calf health and thereby contributing to the high average rate of calf mortality observed in recent years, but it cannot explain the large year-to-year variance in calf deaths since 2000.

Introduction

An individual's health and reproductive success may be strongly affected by many environmental stresses. In baleen whales, nutritional stress, exposure to algal biotoxins, infectious diseases, and various anthropogenic factors have been shown to influence reproduction (Lockyer 1981, 1986, 1987, Aguilar & Borrell 1990, Reeves et al. 2001, Gulland & Hall 2005, Leaper et al. 2006, Leandro et al. 2010, Miller et al. 2011). From 2003 to 2014, at least 626 southern right whale (*Eubalaena australis*) calves died at the Península Valdés calving ground in Argentina with an average of more than 50 deaths per year (International Whaling Commission [IWC] 2011, Rowntree et al. 2013, Sironi et al. 2014). During the previous decade (1993-2002), the average had been 8.2 y^{-1}, with no more than 14 dead calves detected in any year since 1971. Despite considerable research effort since 2003, the cause(s) of the recent high mortality events remain undetermined (IWC 2011, Thomas et al. 2013).

Harassment by Kelp Gulls (*Larus dominicanus*) has been proposed as a potential contributor to the calf deaths (IWC 2011, Thomas et al. 2013). Kelp Gulls at Valdés have learned to feed on the skin and blubber of living right whales (Cummings et al. 1972, Thomas 1988, Rowntree et al. 1998, Fazio 2013, Sironi & Rowntree 2013). During an attack, a gull lands on a whale's back and gouges out skin, either opening a new lesion or enlarging a preexisting one (Thomas 1988, Rowntree et al. 1998). During successive attacks, gulls widen and/or dig more deeply into the dermal and subdermal layers of skin, exposing blubber and creating lesions of various sizes and depths. Kelp Gull attacks usually occur when whales are resting or surfacing to breathe and their backs are fully or partially exposed to the air (Thomas 1988).

Attacks were first reported at Península Valdés in the 1970s when Kelp Gulls occasionally picked sloughed skin from the water or the whales' backs (Cummings et al. 1972). In the 1980s, Thomas et al. (Thomas 1988) described gull attacks as "parasitic" with gulls gashing the skin and underlying blubber of whales in Golfo San José. Mothers were the predominant target, and calves were rarely attacked. In the mid-1990s, both mothers and calves that were followed continuously for an hour were attacked in both gulfs of the peninsula (Golfo San José and Golfo Nuevo) at an average frequency of 17% of the total observation intervals recorded (Rowntree et al. 1998). By 2005-2012, gull attack rates escalated to 24% in both gulfs, and most attacks (69%) were aimed at calves (Sironi & Rowntree 2013). In 2012, some dead calves that stranded on the beaches had 25 or more gull-attack lesions on their backs (Thomas et al. 2013). Kelp Gull harassment has not been observed in any other cetacean population, except for two isolated cases recorded in southern right whales off Brazil in the 1990s (Groch 2001).

Gull harassment negatively affects the behavior, energy expenditure and probably the body condition of mothers and their calves. In 1995, mother-calf pairs harassed by gulls more than tripled the time spent in high-energy activities compared to those that were not attacked. Pairs swam at medium or fast speeds to flee gull attacks, reducing time spent in low-energy activities (e.g., resting and traveling slowly) by 25% (Rowntree et al. 1998). Low-energy activities are the predominant behaviors of lactating right whale mothers at Valdés when not disturbed by gulls (Thomas & Taber 1984, Thomas 1988, Rowntree et al. 1998). Lactating mothers on the calving grounds are fasting and relying on blubber reserves for self-maintenance and nursing. Mothers cannot recover energy reserves spent fleeing gull attacks because food is available only occasionally at Valdés during the calving season (Payne 1995, Sironi 2004, Hoffmeyer et al. 2010). Calf survivorship may be compromised if mothers and calves invest more energy and time fleeing Kelp Gulls than resting and nursing. Constant gull harassment could also increase the metabolic stress of mother-calf pairs while on the calving ground.

In 2013, a workshop was convened to consider possible causes of the high calf mortality at Valdés. The specialists present concluded that Kelp Gull harassment is probably a major stress factor for the whales: “the physical injury of extensive gull lesions can compromise the integrity and impermeability of the whale’s surface layers and lead to dehydration, loss of thermoregulatory capacity, and increased energy outlay to wound healing and metabolic stasis” (Thomas et al. 2013). Thus, gull attacks could negatively affect body condition of mother-calf pairs during a critical period when calves depend on maternal milk for growth and survival.

The intensity of gull attacks on an individual whale can be estimated from the number and size of lesions on its back. Here we focus on the history of wounding in living and dead calves at Península Valdés over the last four decades. We ask specifically whether the increase in wounding rates has been similar for living calves and their mothers, and whether living and dead calves suffered more wounding in years of high calf mortality during the period 2003-2011. We also look for effects of calf age (using body length as a proxy) and location (Golfo San José *versus* Golfo Nuevo) on the intensity of gull attacks.

Materials and Methods

Presence and Number of Lesions on Living Mother-Calf Pairs

To determine the presence, number and size of lesions on living mother-calf pairs, we used photographs taken during annual aerial surveys at Península Valdés in 1974-1979, 1982-1990, 1993, 1995, 1996, 1999, 2000, 2002-2011 (1971-73 and 1980-81 were excluded because of poor photo quality or incomplete survey coverage). Photographs of southern right whales are used to identify individuals through the distinctive callosity patterns on their heads and pigmentation patterns on their backs (Payne et al. 1983). Only photo-identified mothers were selected to avoid recording a mother (or her calf) more than once in a given year. Mothers resighted within two to thirty-seven years were included in the analysis because most lesions disappear within two to four years (Rowntree et al. 1998). Most calves included in the study were not identified because the callosity pattern is not well developed in young calves. Locations of sightings at Valdés were also recorded (Golfo Nuevo, Golfo San José and Outer Coast, see Chapter 2, Fig. 2.1) during the aerial surveys (Payne 1986). Most calves photographed were older than a month and few were newborns because aerial surveys have occurred only once or twice a year since the 1980s (around the time of peak of whale abundance from 15 September to

15 October, Payne 1986, Rowntree et al. 2001), and most calving events occur in August (Whitehead & Payne 1981).

The presence of lesions was scored categorically for each mother and calf as follows: “yes” if the whale had at least one lesion or “no” if it had no lesions. Lesions were scored only if the center of the whale’s back was clearly visible (above water or under water). Whales were scored as having zero lesions (“no”) only if the center of the back and ≥70% of its total area were clearly visible. If the whale had lesions (“yes”) and its back was ≥50% visible, then the total number of lesions was recorded and their shape, placement and size were drawn on a silhouette (Fig. 4.1). We did not count the number of lesions if there were one or more ("yes") but less than 50% of the back was visible. Presence (or absence) of lesions could not be scored in 25% of all right whale mothers photo-identified in 1974-2011 due to their position (underwater, rolling) or poor photo quality. Lesions in calves could not be determined in 41% of all cases due to their position (underwater, hiding below their mothers, nursing, rolling or playing) or poor photo quality.

Presence and Number of Lesions on Dead Calves

To determine the presence, number and size of lesions on dead calves, we used photographs taken during necropsies of calves that died and stranded at Península Valdés in 2003-2011. Although dead calves were in various states of decomposition, only photographs of fresh dead calves without major skin damage (minimal detached skin or damage by scavengers) were selected for this analysis (Uhart et al. 2009). Necropsies were conducted by the Southern Right Whale Health Monitoring Program (SRWHMP) annually throughout the season (June to December). Necropsied calves varied in length (3 to 9 m), age (newborns to calves less than four months old) and stranding location (Golfo Nuevo, Golfo San José and Outer Coast) with most recorded in the gulfs (Uhart et al. 2009, Rowntree et al. 2013, Sironi et al. 2014).

Presence of lesions was determined as described above for living whales: “yes” if the dead calf had lesions or “no” if it had no lesions. We counted and drew lesions on dead calves following the same procedures described above for living mother-calf pairs (backs ≥50% clearly visible and no major skin damage). Presence of gull-inflicted lesions could not be determined in 56% of all recorded calves (*n*=438) that died in 2003-2011 because they were upside down or in advanced states of decay (no skin) or the photographs were of poor quality.

Size of Lesions on Living and Dead Whales

We drew lesions in proportion to the size of the whale’s back using a whale silhouette (Fig. 4.1). Each lesion was assigned to one of seven size categories: extra-small (XS), small (S), medium (M), large (L), extra-large (XL), double XL (XXL) and triple XL (XXXL) (Table 4.1). The smallest lesions, XS, represent the earliest stages of a gull-inflicted lesion, when the skin is pecked enough to make a small amount of blubber visible (Fig. 4.2). The absolute sizes of XS and larger lesions are different for mothers and calves, because they are drawn on the silhouettes in proportion to the size of the individual. Thus the size categories represent relative wound sizes, with XS lesions averaging roughly 1/800 of the area of the back, S averaging roughly 1/400, and so on in a doubling series (Table 4.1). The elongated and continuous XXL and XXXL lesions are formed by the merger of adjacent lesions (Fig. 4.2). XXL lesions are typically less than half as long as the back, while XXXL lesions typically extend along more than half of the length of the back.

Area of Lesions on Living and Dead Whales

Because a whale with three XS lesions is much less damaged than a whale with three XL lesions, we combined the size and total number of lesions to estimate the overall area of lesions (or wounded area), using the XS lesions as the basic unit of measure (Table 4.1). First, each lesion larger than XS was converted into its equivalent number of XS lesions. Then the number of XS-lesion-equivalents was added to represent the total area of lesions. For example, a whale that had one XS lesion and one M lesion (number of lesions = 2) was considered to have a total area of five XS lesions because one M lesion is roughly equivalent to four XS lesions.

Percentage of Back Damaged on Living and Dead Whales

To determine the percentage of the whale's back that is damaged by lesions, we used ImageJ (Rasband) to analyze 15 living calves (1974-2011) that had >80% of their backs clearly visible above water. Using the same whale silhouette to draw the lesions (Fig. 4.1), we drew an oval representing the total back area (TBA) that extends from the fat roll (immediately behind the blowholes) to the beginning of the tail stock and laterally to the "shoulders" (dotted line, Fig. 4.1). For each calf, we calculated the TBA in pixels which represents 100% of its back. Then, we calculated in pixels the total area of all lesions of different sizes (solid lines) and then divided it by the TBA to estimate the percentage of back damage. Finally, to establish a scaling between XS-equivalents and the percentage of the whale’s back area that is damaged, we calculated the area in pixels of all the XS lesions present on all 15 calves. The average pixel area of all XS lesions was divided by TBA to estimate the percentage of the back damaged by one XS lesion. We then multiplied that percentage by the numbers of XS-equivalents to estimate the standard conversion factors summarized in Table 4.1.

Changes in the Number and Area of Lesions with Calf Age

Calf length can be used to estimate calf age (Best 1981, Whitehead & Payne 1981, Best & Rüther 1992, Rowntree et al. 2013). We used calf length to ask whether lesion numbers and areas increased with calf age in dead and living calves. Although calving occurs from June to November (Whitehead & Payne 1981, Uhart et al. 2008), most calves are born in August at an average length of 5.5 m and grow as much as 3 m (Best & Rüther 1992) during their three months on the calving ground (Taber & Thomas 1982, Thomas & Taber 1984). However, some calves are shorter than 6 m when born, and they predominate among those that died early in the calving season (before October 1) (Rowntree et al. 2013, Table 4.2). Conversely, calves larger than 6 m are usually among those that died late in the season (on or after 1 October) (Best & Rüther 1992, Rowntree et al. 2013) (Table 4.2). We considered dead calves <6 m to be “small” and those ≥6 m to be “large.” Dead calf lengths were determined with a tape measure as a straight line from snout to fluke notch and were recorded by the SRWHMP during necropsies of dead calves following standard procedures (McLellan et al. 2004, Geraci & Lounsbury 2005). Data for gull-lesion analysis were collected at Valdés in 2003-2011.

Living calves off South Africa average 40% of their mothers’ lengths at the beginning of the calving season (late July) and increase to 51% of their mothers’ lengths later in the season (mid-October, Best & Rüther 1992). Because length measurements were not available for living calves at Península Valdés, we used the ratio of calf to mother body lengths to examine differences in wounding patterns in young *versus* older calves. Living calves less than 50% their mother’s length were considered to be “small” and those greater than 50% of their mother’s length were considered to be “large.” Calf length estimates were calculated from aerial survey photographs in the ‘90s and 2000s (1993, 1995, 1996, 1999, 2000, 2002-2011).

Changes in the Number and Area of Lesions in High and Low Mortality Years

We asked whether calves (living and dead) in high mortality years had lesions covering larger areas than calves of similar length in low mortality years. We defined high mortality and low mortality years in the 2000s following Rowntree et al. (2013). Briefly, in low mortality years (2004 and 2006) the number of dead calves was not significantly greater than expected based on the population’s long-term growth rate, while in high mortality years (2005, 2007-2011) the number of dead calves was significantly greater than expected.

Statistical Analyses

R software version 3.1.1 (R Core Team 2013) was used for all statistical analyses. Contingency chi-square tests and one-way ANOVAs were used to determine changes in the intensity of wounding in living mother-calf pairs photographed in aerial surveys from 1974 to 2011. Specifically, the presence, number and area of lesions on living pairs were compared among decades, gulfs (Golfo Nuevo and Golfo San José) and calf length (small or large). Living mothers and calves sighted on the Outer Coast were excluded when comparing number and area of lesions per gulf (Golfo Nuevo and Golfo San José) because few mother-calf pairs have been recorded there since the 1980s (Rowntree et al. 2001). However, living mothers and calves sighted on the Outer Coast were included in other comparisons. Additionally, the numbers and areas of lesions were compared in living calves in high *versus* low mortality years controlling by calf length (factor variable: "small" *versus* "large" calves).

Linear regression and Kendall's rank correlation were used to evaluate changes in the intensity of wounding in dead calves photographed during necropsies from 2003 to 2011. Specifically, the numbers and areas of lesions were compared in dead calves among gulfs (excluding the Outer Coast), in high *versus* low mortality years, and in small *versus* large calves. We adjusted by calf length (using the numerical measurements) when comparing lesions among gulfs and mortality levels.

Results

Increased Presence of Lesions on Living Mother-Calf Pairs

The presence of gull lesions was assessed in 2680 living whales (1527 mothers and 1153 calves) photographed during aerial surveys in 1974-2011. The proportions of mothers and calves with lesions increased through the four decades (Fig. 4.3, Table 4.3). Gull-inflicted lesions were rarely seen on mother-calf pairs in the 1970s (2% of pairs examined) but became frequent in the ‘80s (36%), continued to increase in the ‘90s (84%) and became nearly universal in the 2000s (99%) (Table 4.3). These differences are all highly significant (chi-square tests for pairs of decades, or for the whole table).

Increased Number and Area of Lesions on Living Mother-Calf Pairs

The numbers and areas of lesions on living mothers and calves were highly variable among years (Fig. 4.4a, 4.4b, 4.4c and 4.4d) and decades (Table 4.4) with a tendency to increase over time. However, comparatively more lesions were recorded on calves in the 2000s than on mothers (Table 4.4). Typical calves had no lesions in the ‘70s and ‘80s, but an average of around nine lesions in the 2000s (Table 4.4). The numbers of lesions on mothers increased from an average of zero in the ‘70s to two in the ‘80s and three or four in the ‘90s and 2000s. The average area of lesions also increased from the ‘70s to the 2000s, from zero to 20 XS-equivalents in calves and zero to seven XS-equivalents in mothers. The largest numbers ever recorded were 22 in mothers and 34 in calves, and the largest areas were 44 XS-equivalents in mothers and 147 XS-equivalents in calves. A total area of 147 XS lesions on a calf is roughly 19% of its back (Table 4.1).

In the 2000s, the gulf with more wounding changed from Golfo San José to Golfo Nuevo (Fig. 4.5a, 4.5b, 4.5c and 4.5d). In the ‘70s, ‘80s and ‘90s, mothers and calves surveyed in Golfo Nuevo had significantly fewer lesions and smaller wounded areas than those in Golfo San José (ANOVA, number and area of lesions in mothers: all p -values < 0.001, number and area of lesions in calves: all p -values ≤ 0.01) (Fig. 4.5a and 4.5b, Table 4.5). However, by the 2000s, mothers surveyed in Golfo Nuevo had more and larger lesions (ANOVA, $p = 0.01$); calves showed the same trend, but it was not significant (ANOVA, p = 0.70) (Fig. 4.5a and 4.5b, Table 4.5).

Both calf length relative to mother and number of lesions were determined in 565 living calves photographed from 1993 to 2011, 87% of which were large calves. Large living calves had more lesions (mean ± SD, 8.61 ± 5.33) than small calves (7.07 ± 4.65) (ANOVA, p = 0.02), but their area of lesions was not significantly larger (ANOVA, p = 0.17). However, both the number and wounded area were significantly larger in large living calves when limiting the comparison to calves within the 2000s (2003-2011) (ANOVA, number of lesions: $p < 0.001$, lesion area: $p = 0.01$). Although the numbers of lesions were higher in low (n=88) than in high (n=238) mortality years for calves of similar length (regression, number of lesions p = 0.002), there were no significant differences in the area of lesions among low and high mortality years (regression, area of lesions: p = 0.74).

Increased Presence, Number and Area of Lesions on Dead Calves

Presence of lesions was assessed in 192 dead calves photographed during necropsies from 2003 to 2011 at Valdés (Table 4.3). Similar percentages of dead calves were found with gull-inflicted lesions (56.3%) and without them (43.7%). Compared to living calves, number (n=186) and area (n=177) of lesions were determined in fewer dead calves because of poor photo quality, back exposure or skin decay. The average number of lesions on dead calves was four (range: zero to 21) and the average wounded area was 10 XS-equivalents (range: zero to 79) (Table 4.4). An area of 79 XS lesions on calves is roughly 10% of the back damaged by gull lesions (Table 4.1).

Both calf length and number of lesions were determined in 181 dead calves that stranded at Valdés in 2003-2011, 44% of which were large calves. The lengths ranged from 3.64 to 8.80 m. Both lesion number and lesion area increased with calf length (Fig. 4.6a and 4.6b) (Kendall's rank correlation; number of lesions $p < 0.001$; area of lesions $p < 0.001$).

Numbers and areas of lesions on dead calves increased from 2003 to 2011 (Fig. 4.7a and 4.7b). However, adjusting by calf length, there were no significant differences in the number or area of lesions among low (n=12) and high (n=174) mortality years (Fig. 4.6a and 4.6b) (regression, number of lesions $p = 0.23$, area of lesions: $p = 0.26$). When controlling by calf length, dead calves that stranded in Golfo Nuevo (n=139) had larger numbers and wounded areas compared to those that stranded in Golfo San José (n=46) in 2003-2011 (regression, number of lesions $p = 0.05$, area of lesions p =0.02, Table 4.6).

Discussion

With almost no exceptions, gull harrassment of right whales has been observed only at Península Valdés. Thus, it could potentially contribute to the recent high calf mortality events. However, the impact of gull-inflicted lesions on whales has not been fully characterized. We have quantified the increased wounding of mothers and calves over four decades of study. We find that the first pairs documented to have gull-inflicted lesions were photographed in the 1970s and that calves have recently become the main targets of attacks.

Increasing proportions of right-whale mother-calf pairs have gull-inflicted lesions on their backs at Península Valdés. In the 1970s, most living mother-calf pairs were lesion-free. By the 1980s, around a third of pairs carried lesions. In the 1990s, the proportion of pairs with lesions increased significantly and by the 2000s, almost every mother-calf pair had lesions. This finding, from retrospective analysis of aerial survey photographs, supports behavioral studies that find higher frequencies of gull attacks in the 2000s than in previous decades (Sironi et al. 2009, Sironi & Rowntree 2013).

The increased incidence of gull-inflicted lesions on calves as compared to their mothers has not previously been noted. While the number of lesions on living mothers has remained nearly the same with an average of two to four lesions through the ‘80s, ‘90s and 2000s, the number of lesions on living calves has greatly increased from an average of one lesion in the ‘80s to nine lesions in the 2000s. In addition, the area of lesions on living calves has increased dramatically from an equivalent of two extra-small lesions in the ‘80s to 20 extra-small lesions in the 2000s, which is three times the damaged (relative) area on living mothers in the same years. The largest area of lesions recorded for a living calf covered 19% of its back.

Mothers appear to have learned how to defend themselves. The lack of change in number and area of lesions on mothers may be explained by their adopting a variety of resting and breathing postures that help them evade gull attacks (Thomas 1988, Sironi et al. 2009). Until the late 1980s, mothers were often seen resting at the surface (even for an hour or more) and their backs dried out, exposing peeling skin that was pecked off by Kelp Gulls (Thomas 1988). However, since the mid-1990s, mothers with dry backs are rarely seen because they have adopted avoidance postures such as the “galleon.” In the galleon posture (or “crocodiling” according to Thomas 1988), mothers arch their backs exposing only their heads and tail flukes above water. The galleon position was first documented in 1984 (Thomas 1988) and has spread through the adult population (Sironi et al. 2009).

Unlike mothers, calves have not developed as many avoidance postures and may be more vulnerable to gull attacks. They have shorter backs (compared to adults and juveniles) and may therefore find it difficult to arch their bodies deeply enough to keep below the surface. Perhaps more fundamentally, calves have never experienced Kelp-Gull attacks, while their mothers have had many seasons on the Valdés calving ground to learn about them. Calves surface to breathe much more frequently than adults (Sironi & Rowntree 2013), so their backs are exposed more often than older whales. Since the 2000s, some calves (and also mothers) have learned to surface at an oblique angle to blow while keeping their backs underwater ("oblique breathing" Fazio et al. 2014). Oblique breathing may minimize the impact of gull attacks but could also be energetically costly for newborns or young calves (Fazio et al. 2014). Thus avoiding gull attacks seems likely to be more energetically costly for calves (e.g., swimming away at fast speeds, Rowntree et al. 1998, or perform oblique breathing, Fazio et al. 2014) than for mothers, in a period when most of their energy is needed for growth, development and play (Thomas & Taber 1984).

Dead calves did not have larger lesions in high mortality years than in low mortality years in the period 2003-2011 (Fig. 4.7a and 4.7b), nor did living calves (Fig. 4.4c and 4.4d). Furthermore, living calves had more lesions in low mortality years for the same time period. Thus the dramatic year-to-year variation in calf mortality rates during the 2000s is not explained by the apparently modest year-to-year variation in gull-lesion rates. This implies that other, still unidentified factors must contribute to the high rates of calf mortality seen in some years. In principle, chronic and roughly constant stresses caused by Kelp Gull attacks could sensitize calves to these other factors, which otherwise might cause relatively little mortality. However, it is striking that only 20 calves died at Valdés in 2014, the year with the lowest gull attack frequency (19.2%) in Golfo Nuevo since 2006 (average frequency for 2005-2013 was 28%, Sironi & Rowntree 2013, M. Sironi pers. comm.).

The intensity of wounding is currently higher in Golfo Nuevo than in Golfo San José. Solitary adults, juveniles and mother-calf pairs with lesions were rarely seen in Golfo Nuevo until 1986 (Rowntree et al. 1998). We found that from the 1970s to the 1990s, larger numbers and areas of lesions were recorded on living mother-calf pairs sighted in Golfo San José, but by the 2000s more lesions were recorded in Golfo Nuevo. More lesions were also found on dead calves that stranded in Golfo Nuevo in the 2000s compared to those in Golfo San José. The increase in wounding in Golfo Nuevo seen here from retrospective analysis of aerial survey photos supports previous behavioral observations of higher gull attack frequencies in Golfo Nuevo compared to Golfo San José in the 2000s. From 2005 to 2013, the average frequency of attacks in Golfo Nuevo (28%) was almost 50% higher than in Golfo San José (19%) (Sironi & Rowntree 2013). Interestingly, most (76%) calves that died at Valdés in 2003-2011 were found in Golfo Nuevo. This could result in part from a net movement of whales from Golfo San José to Nuevo, or from other habitat differences (Rowntree et al. 2013). However, it also coincides with higher attack frequencies and wounding in Golfo Nuevo (Sironi & Rowntree 2013 and findings presented here).

Larger calves (living and dead) tend to have more and larger lesions than small calves. Most small living and dead calves without lesions were probably newborns. The increased wounding with calf length (~age) confirms Thomas' (Thomas 1988) observation that gull lesions on living mothers increased in size through the season. If calves have become the preferred targets of Kelp Gulls, then the longer calves remain at Valdés the greater may be the energetic costs they suffer, with potentially significant effects on survival.

Numbers and areas of lesions were not compared for living *versus* dead calves because there are many differences between the two samples. First, data collection occurs over different time frames, so the samples have different age distributions. Data collection for living calves occurs over a two-day period in September or early October when most calves are at least one month old. However, data collection for dead calves occurs from June through December, and includes all ages from newborns to calves nine m in length. The majority (87%) of living calves that could be examined for gull lesions were large (≥50% their mother's length), but only half (44%) of dead calves examined for gull lesions were large (≥6 m). Second, the effort to count and record gull-inflicted lesions in dead calves increased since 2007, while the aerial survey effort to sample living whales has not changed much since the 1980s. Most necropsy reports previous to 2007 do not include enough detail about the number and size of gull lesions and few photographs were taken during external assessments. For example, lesions were not recorded for the majority of dead calves that stranded in 2003 and 2006. Third, a smaller proportion of dead calves (44%) than living calves (59%) were included in the gull lesion analyses presented here, owing mainly to their stranded position, state of decomposition, and in fewer cases, poor photo quality. The percentage is even smaller for number and area of lesions (~40%) for these same reasons. Thus, our results about presence of lesions in dead calves represent less than half of all the calves found dead at Valdés. These limitations cannot be overcome because dead whales are usually found in advanced states of decomposition and with major skin loss or damage (Uhart et al. 2009).

The depths of lesions have been little studied, but could be an important factor determining the damage from gull attacks. In contrast to lesions on the epidermis, lesions that reach more deeply into highly vascularized layers such as the dermis or the hypodermis (Reeb et al. 2007) are more likely to facilitate fluid loss. Most gull-inflicted lesions analyzed in dead right whales at Valdés were present in both the epidermis and dermis and a few penetrated to the underlying hypodermis (D. McAloose et al. submitted). When analyzing a sequence of aerial photographs of a living mother in 1999, we observed a Kelp Gull repeatedly gouge pieces of blubber from a lesion until it began to bleed. Unfortunately, we are not able to measure lesion depth in photographs of living whales, but since 2013, the SRWHMP has been taking three-dimensional measurements of wounds (number, size and depth) on dead calves. Further research is needed to improve our understanding of the severity of gull lesions in individual whales.

Evidence that similar types of parasite harassment can lead to fatigue and stress in mammals is accumulating for lions, and for wild and domestic ungulates. Die-offs of these other large mammals have been associated with biting by *Stomoxys* flies (Mihok & Clausen 1996, Elkan et al. 2009, Barros et al. 2010). Kelp Gulls usually chase the whales by flying over them or resting on the water until they surface to breathe and then continue their attacks. Continuous harassment could potentially increase stress levels in mothers and calves and could negatively affect their body condition. Gull attacks on single mother-calf pairs can go on for more than an hour (Rowntree et al. 1998). Further research is needed to evaluate whether gull attacks increase the whales' metabolic stress and compromise their body condition and overall welfare.

Gull harassment could impact calf survivorship if calves invest more energy avoiding gull attacks and healing wounds than playing, resting and nursing. Swimming and play are the most frequent activities of undisturbed calves, and play may be critical for developing the strength and motor skills needed for migration to the feeding grounds (Thomas & Taber 1984). Play may also be important for the development of adult behavior and social skills for survival and successful reproduction (Thomas & Taber 1984, Spinka et al. 2001), as well as promoting general neural and muscular development in calves as described for other mammals (Byers & Walker 1995, Byers 1998).

Mothers rest more than calves at Península Valdés (Thomas & Taber 1984), but periodic rests may also help calves allocate energy to growth. Mothers frequently stop calf play, perhaps to conserve energy (Thomas & Taber 1984). Both playing and resting increase with calf length (Thomas & Taber 1984), suggesting that they are essential to normal development. Kelp Gull attacks were previously shown to increase the time invested in swimming at medium and faster speeds by almost fourfold, and to reduce the time spent in resting and swimming slowly by 25% (Rowntree et al. 1998).

Since the 1990s, mothers have learned to evade gull attacks but calves have not, and the numbers and sizes of lesions on calves have continued to increase. Kelp Gull harassment has clearly become a significant threat to the health and welfare of the Península Valdés right whale population. How best to mitigate that threat is not obvious, but a project to cull the Kelp Gull population at Valdés was initiated in 2012 by the provincial government of Chubut in collaboration with researchers from Centro Nacional

Patagónico (CENPAT-CONICET). Continuing the long-term data series that were used here will greatly facilitate efforts to evaluate the effectiveness of this culling.

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Table 4.1. Sizes of gull lesions on southern right whales and their equivalent number of extra-small lesions. [a]Abbreviations: Extra-small (XS), Small (S), Medium (M), Large (L), Extra-large (XL), Double XL (XXL) and Triple XL (XXXL). [b]The total back area or TBA (100%) available for scoring extended from the fat roll (behind the blowholes) to the beginning of the tail stock and down the sides to the region of the back that is above the water or clearly visible through the water when the whale is close to the surface (see Fig. 4.1). See methods for a complete explanation.

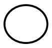
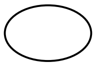
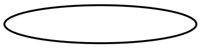
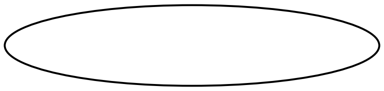
Size[a]	**Description**	**Drawing**	**Equivalent number of XS**	**Estimated percentage of the whale's back damaged**[b]
Extra-small (XS)	Smallest lesion recorded		1	0.13%
Small (S)	2X extra-small		2	0.27%
Medium (M)	2X small		4	0.53%
Large (L)	2X medium		8	1.07%
Extra-large (XL)	2X large		16	2.14%
Double XL (XXL)	Elongated lesion		32	4.28%
Triple XL (XXXL)	Elongated lesion		64	8.55%

Table 4.2. Percent of small (<6 m) and large (≥6 m) dead calves by month (*n*=569). Calf lengths were measured in meters as the straight-line distance from snout-tip to fluke notch. Data were collected at Península Valdés in 2003-2014 (notice that data for gull-lesion analysis was collected only in 2003-2011).

Length *(m)*	**June** (*n*=3)	**July** (*n*=30)	**August** (*n*=142)	**September** (*n*=153)	**October** (*n*=149)	**November** (*n*=75)	**December** (*n*=17)
% <6 m	100	86.67	73.24	63.40	39.60	30.67	29.41
% ≥6 m	0	13.33	26.76	36.60	60.40	69.33	70.59

Table 4.3. Percent of living mother-calf pairs and dead calves with and without lesions by decade. Sample size is indicated between parentheses. Data were collected from aerial survey photographs of living mother-calf pairs in 1974-2011 and necropsy photographs of dead calves in 2003-2011. NA: no data available.

Decade	**Live mothers and calves without lesions**	**Live mothers and calves with lesions**	**Dead calves without lesions**	**Dead calves with lesions**
1970s	97.9% (*n*=231)	2.1% (*n*=5)	NA	NA
1980s	61.6% (*n*=297)	38.4% (*n*=185)	NA	NA
1990s	16.4% (*n*=105)	83.6% (*n*=536)	NA	NA
2000s	1.1% (*n*=14)	98.9% (*n*=1307)	43.7% (*n*=84)	56.3% (*n*=108)

Table 4.4. Wounding of living mothers, living calves and dead calves by decade (1970s-2000s). Mean and standard deviation of number and area of lesions are shown for whales sighted over four decades of study. All means were significantly different among decades for living mothers and calves with the exception of living calves in the ‘70s and ‘80s. *p*-values for comparisons among decades (ANOVA) are to the right of the number and area columns. Sample size is indicated between parentheses. Data were collected using aerial photographs from 1974 to 2011 for living mother-calf pairs and necropsy photographs from 2003 to 2011 for dead calves. NA: no data available.

Decade	**Living mothers**				**Living calves**				**Dead calves**	
	Number	p-value	Area	p-value	Number	p-value	Area	p-value	Number	Area
1970s	0.03±0.22 (*n*=143)		0.06±0.41 (*n*=143)		0.04±0.42 (*n*=92)		0.09±0.83 (*n*=92)		NA	NA
		0		0		0.4		0.8		
1980s	1.80±2.85 (*n*=282)		2.79±4.41 (*n*=282)		0.90±2.08 (*n*=198)		1.46±3.35 (*n*=198)		NA	NA
		0		<0.001		0		0		
1990s	3.49±2.96 (*n*=344)		4.75±3.96 (*n*=344)		5.36±5.35 (*n*=244)		8.24±12.22 (*n*=244)		NA	NA
		0.01		0		0.01		0		
2000s	4.04±2.67 (*n*=592)		6.65±5.10 (*n*=592)		9.19±5.04 (*n*=390)		19.61±15.71 (*n*=390)		3.54±4.42 (*n*=186)	9.75±13.94 (*n*=177)

Table 4.5. Wounding of living mothers (a) and calves (b) by location. Mean and standard deviation of number and area of lesions are shown for whales sighted at Golfo San José and Golfo Nuevo. *p*-values (ANOVA) comparisons among gulfs are to the right of the number and area columns. Sample size is indicated between parentheses. Data were collected using aerial photographs in 1974-2011.

a)

Decade	**Number of lesions on living mothers**			**Area of lesions on living mothers**		
	Golfo San José	Golfo Nuevo	p-value	Golfo San José	Golfo Nuevo	p-value
1970s	0.08±0.35 (*n*=39)	0.00±0.00 (*n*=8)	<0.001	0.13±0.66 (*n*=39)	0.00±0.00 (*n*=8)	<0.001
1980s	4.18±3.53 (*n*=98)	0.58±1.12 (*n*=159)	<0.0001	6.64±5.42 (*n*=98)	0.82±1.53 (*n*=159)	<0.0001
1990s	2.46±2.64 (*n*=39)	0.84±1.12 (*n*=38)	<0.001	3.95±3.66 (*n*=39)	1.45±2.05 (*n*=38)	<0.001
2000s	3.38±1.98 (*n*=234)	4.22±2.16 (*n*=242)	<0.001	5.71±4.53 (*n*=234)	6.82±4.93 (*n*=242)	0.01

b)

Decade	**Number of lesions on living calves**			**Area of lesions on living calves**		
	Golfo San José	Golfo Nuevo	p-value	Golfo San José	Golfo Nuevo	p-value
1970s	0.14±0.74 (*n*=29)	0.00±0.00 (*n*=6)	<0.001	0.28±1.49 (*n*=29)	0.00±0.00 (*n*=6)	0.01
1980s	2.22±2.85 (*n*=73)	0.15±0.77 (*n*=103)	<0.0001	3.68±4.66 (*n*=73)	0.18±0.87 (*n*=103)	<0.0001
1990s	1.93±2.31 (*n*=29)	0.28±1.17 (*n*=32)	<0.001	3.24±3.73 (*n*=29)	0.56±2.34 (*n*=32)	<0.001
2000s	8.67±5.05 (*n*=178)	9.57±4.98 (*n*=143)	0.11	19.47±16.41 (*n*=178)	20.15±14.77 (*n*=143)	0.7

Table 4.6. Wounding of dead calves by location. Mean and standard deviation of number and area of lesions are shown for calves that stranded at Golfo San José and Golfo Nuevo. Sample size is indicated between parentheses. Data were collected using necropsy photographs of dead calves in 2003-2011.

Gulf	**Lesions on dead calves**	
	Number	Area
Golfo San José	1.85±3.18 (*n*=46)	4.00±7.58 (*n*=43)
Golfo Nuevo	4.13±4.64 (*n*=139)	11.68±15.02 (*n*=133)

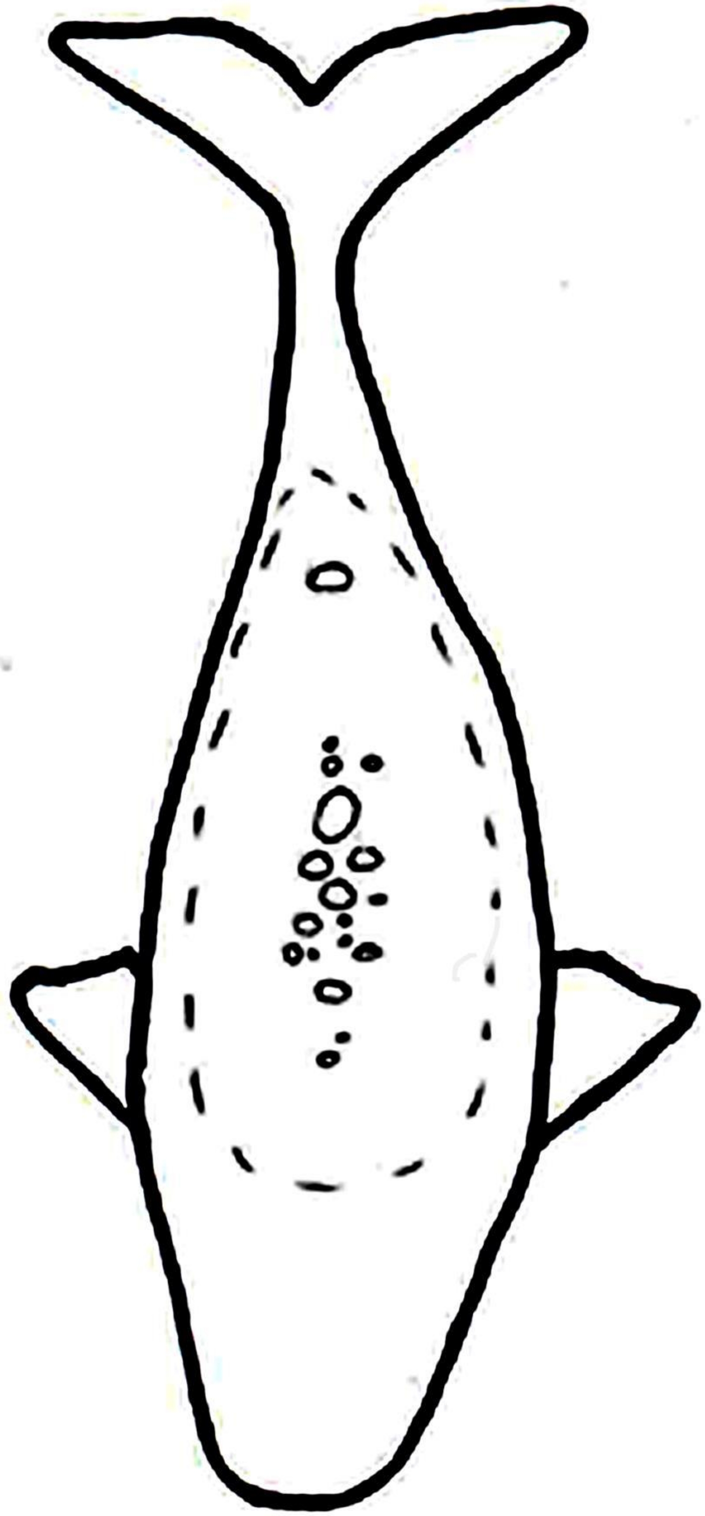


Fig. 4.1. Gull-inflicted lesions on a whale silhouette. The drawing shows the total back area (TBA) that extends from the fat roll to the beginning of the tail stock and laterally to the “shoulders” (dotted line) and lesions of different sizes (solid lines, circles).

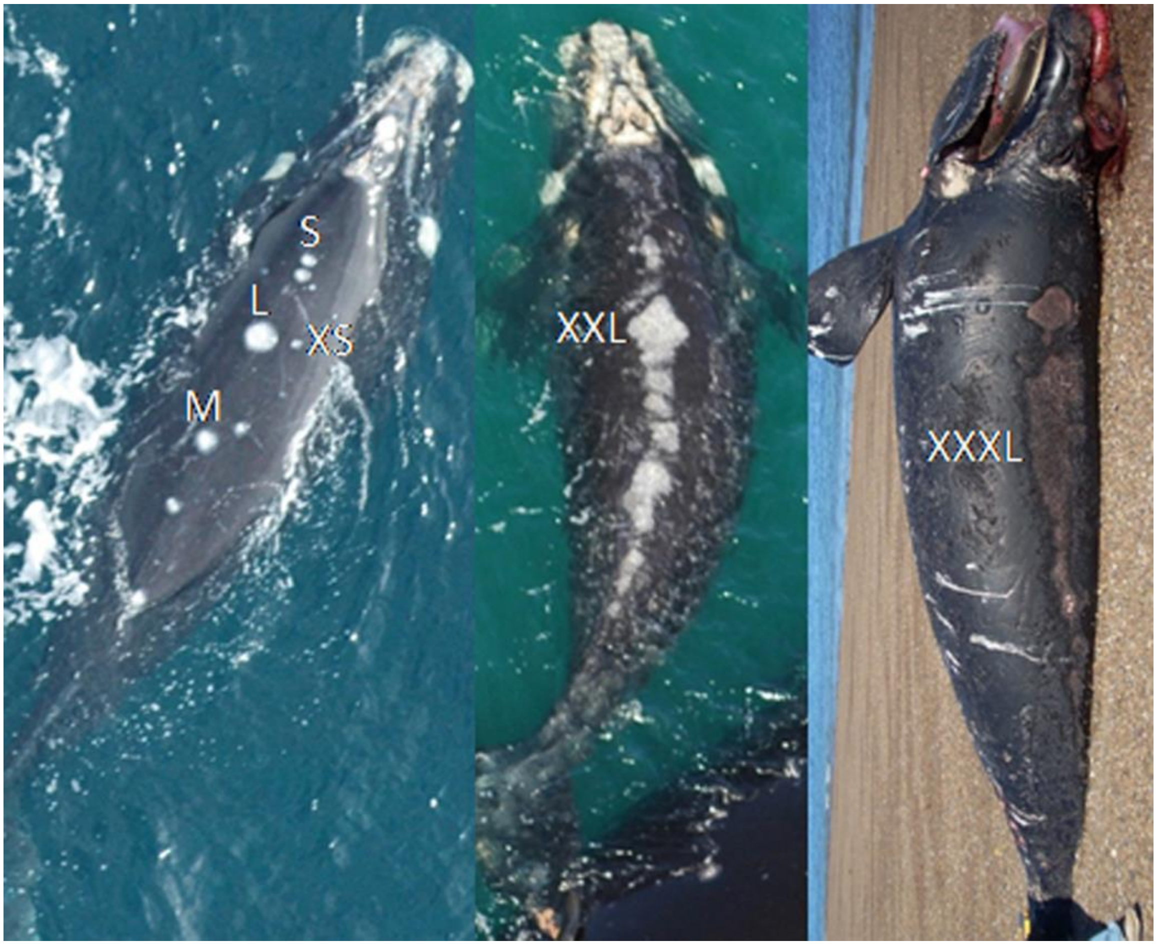


Fig. 4.2. Size of gull lesions. Sizes are shown on the backs of two living (left and middle) and a dead calf (right) photographed at Península Valdés. Each size is indicated by its abbreviation: Extra-small (XS), Small (S), Medium (M), Large (L), Extra-large (XL) and Triple XL (XXXL). Photo credit Ocean Alliance.

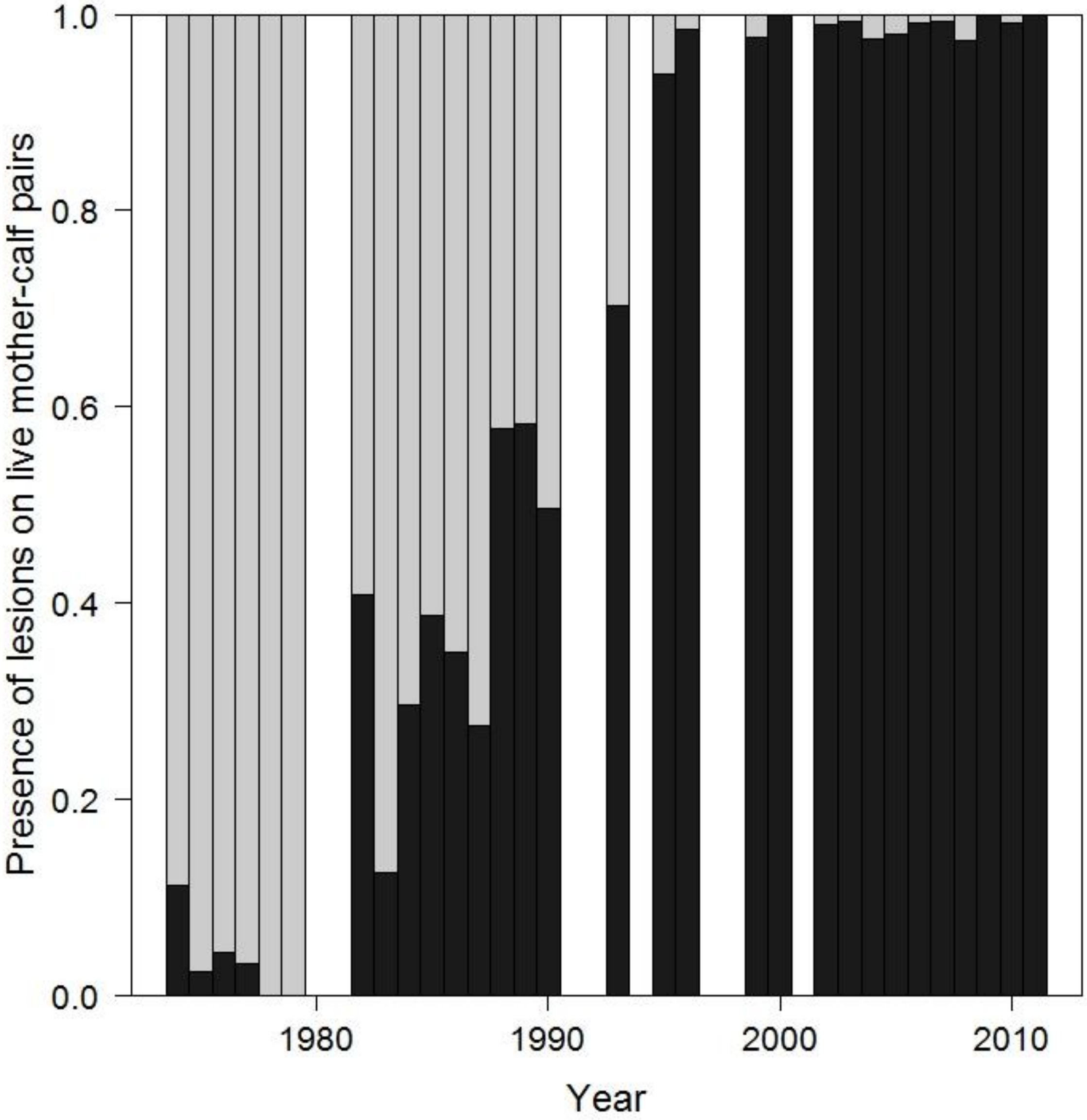


Fig. 4.3. Presence of lesions on living mother-calf pairs in 1974-2011. Light grey bars indicate the proportion of whales without lesions and dark grey bars indicate the proportion of whales with lesions. White columns indicate years excluded from the study.

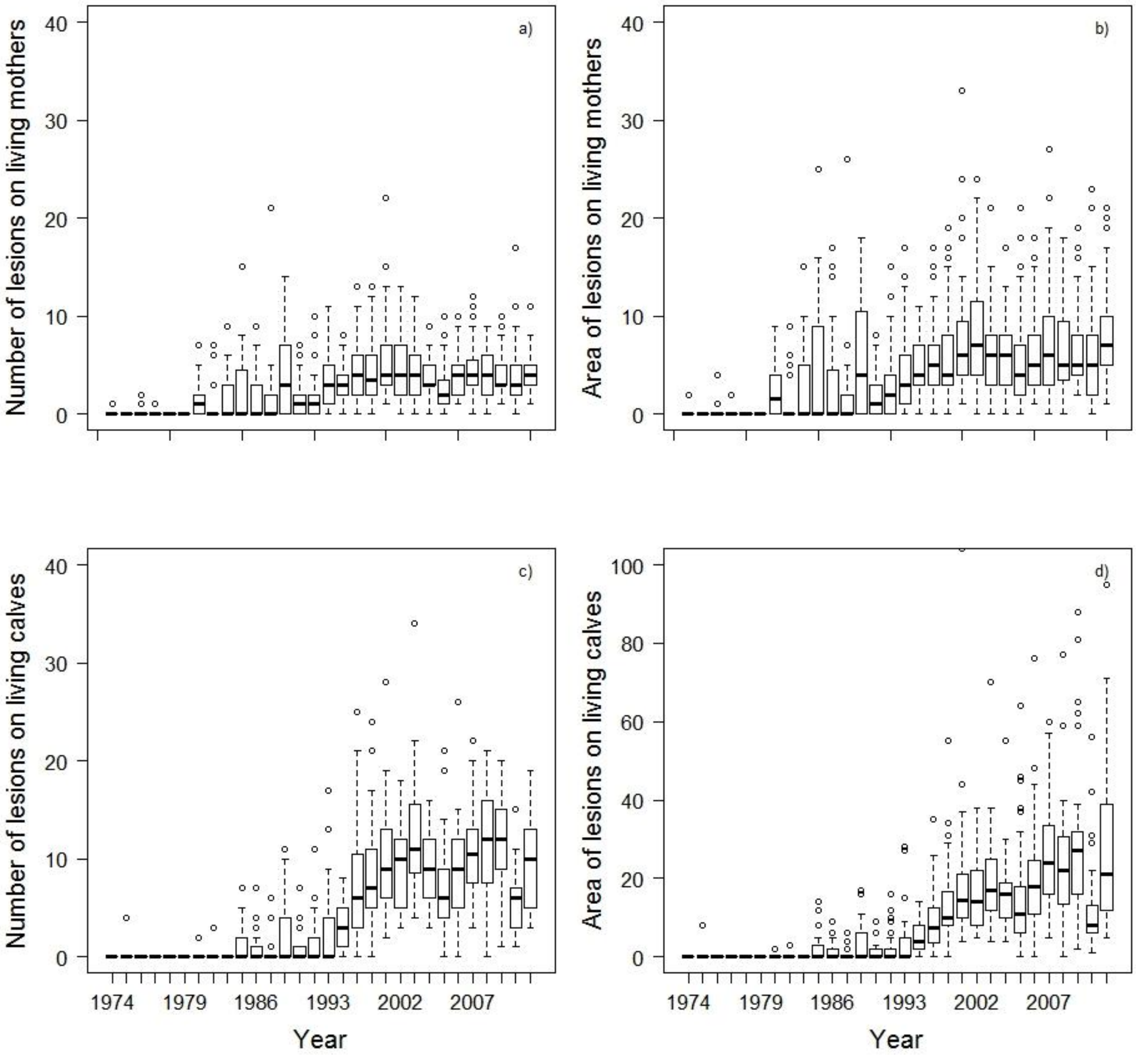


Fig. 4.4. Mean number and area of lesions on living mothers (a, b) and calves (c, d) in 1974-2011. Note the different scale for the y axis in the area of lesions on calves (d). To avoid excessively expanding the y-axis in Fig. 4.4d, two extreme values (y=104 and y=147 XS lesions) were excluded.

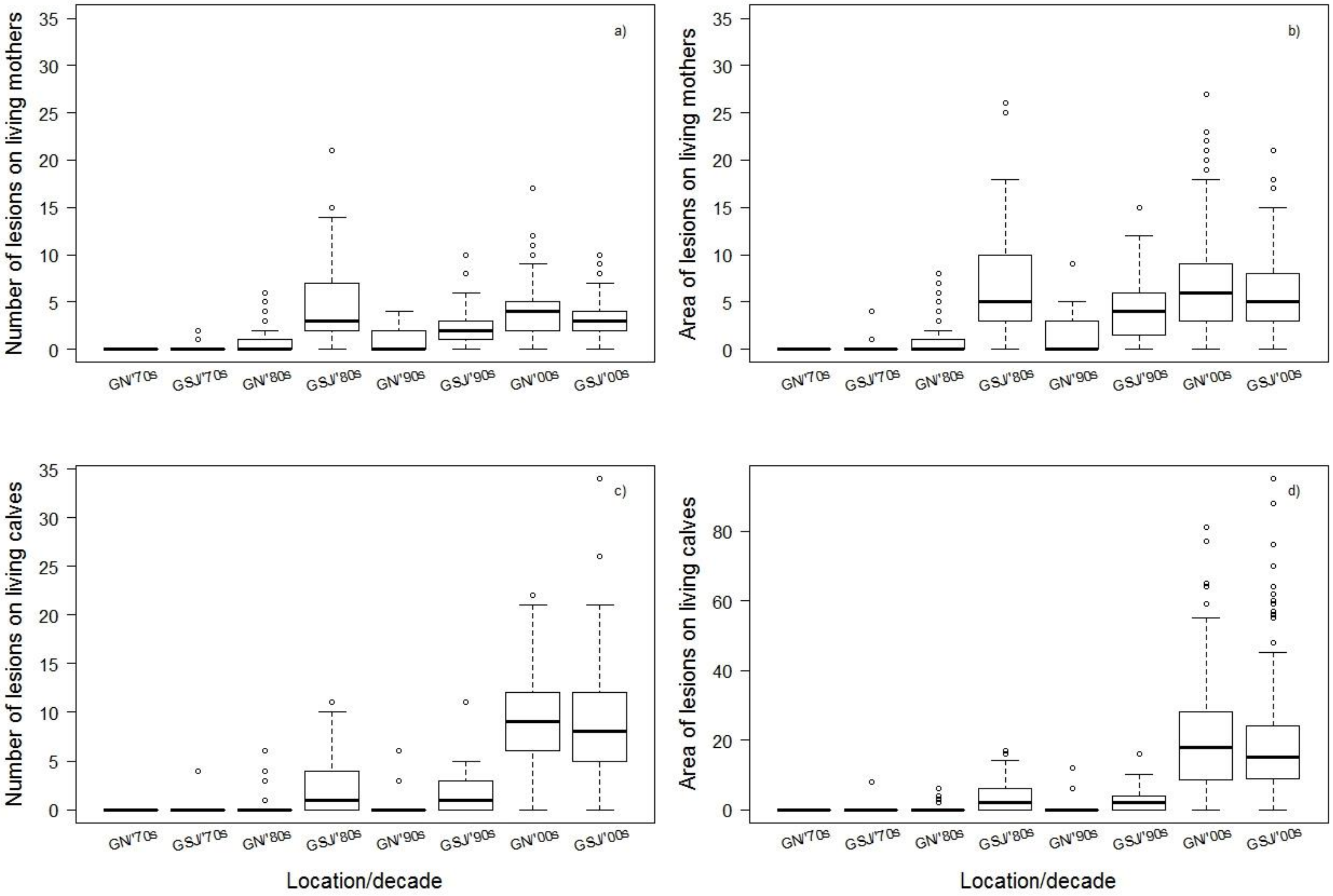


Fig. 4.5. Mean number of lesions on living mothers (a, b) and calves (c, d) by decade and location (GN: Golfo Nuevo, GSJ: Golfo San José).

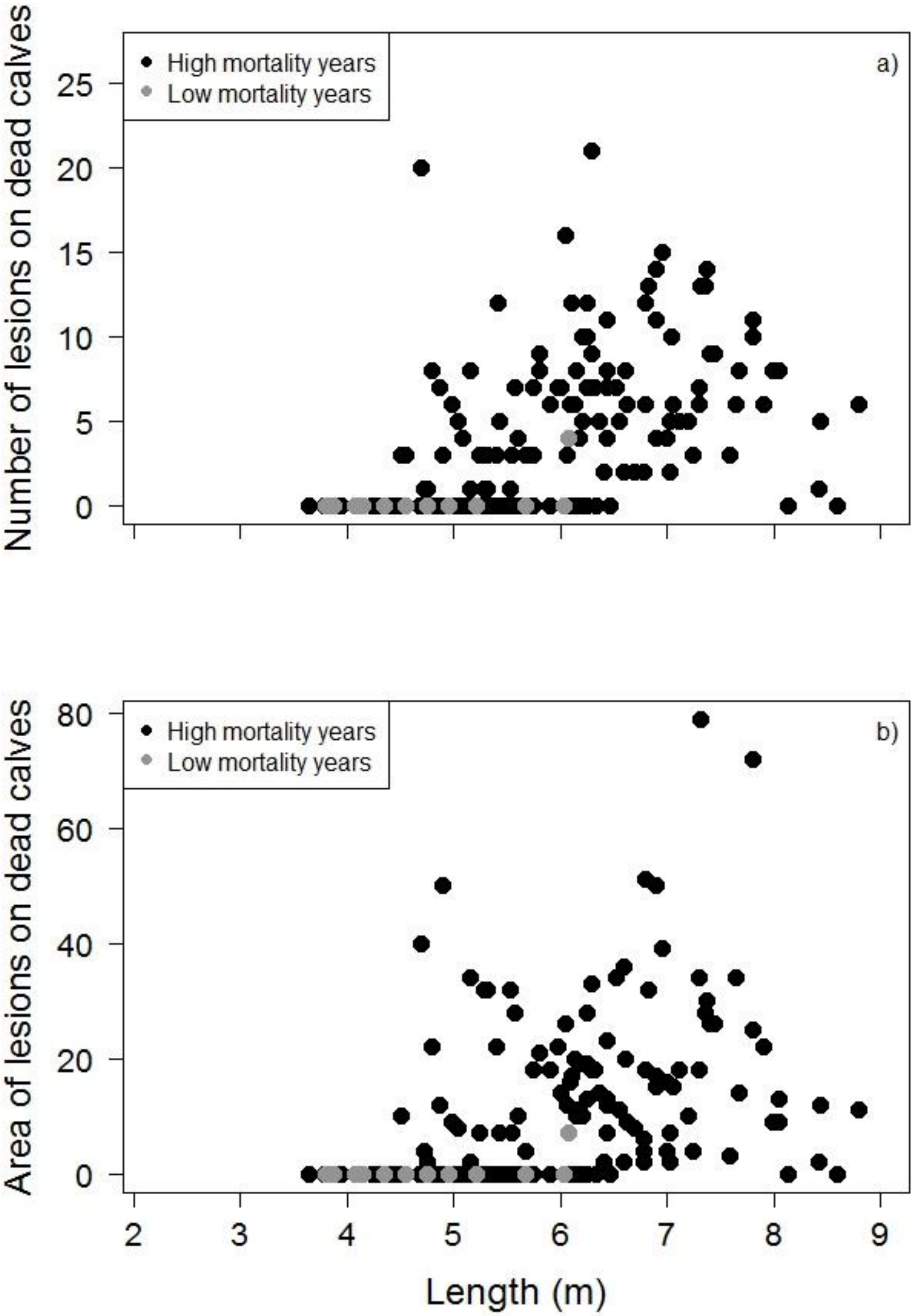


Fig. 4.6. Numbers (a) and areas (b) of lesions by dead calf length in the period 2003-2011. Calves' length ranged from 3.64 to 8.80 m. Grey dots indicate calves that died in low mortality years (*n*=12) and black dots indicate calves that died in high mortality years (*n*=174). Kendall's rank correlation, $p < 0.001$.

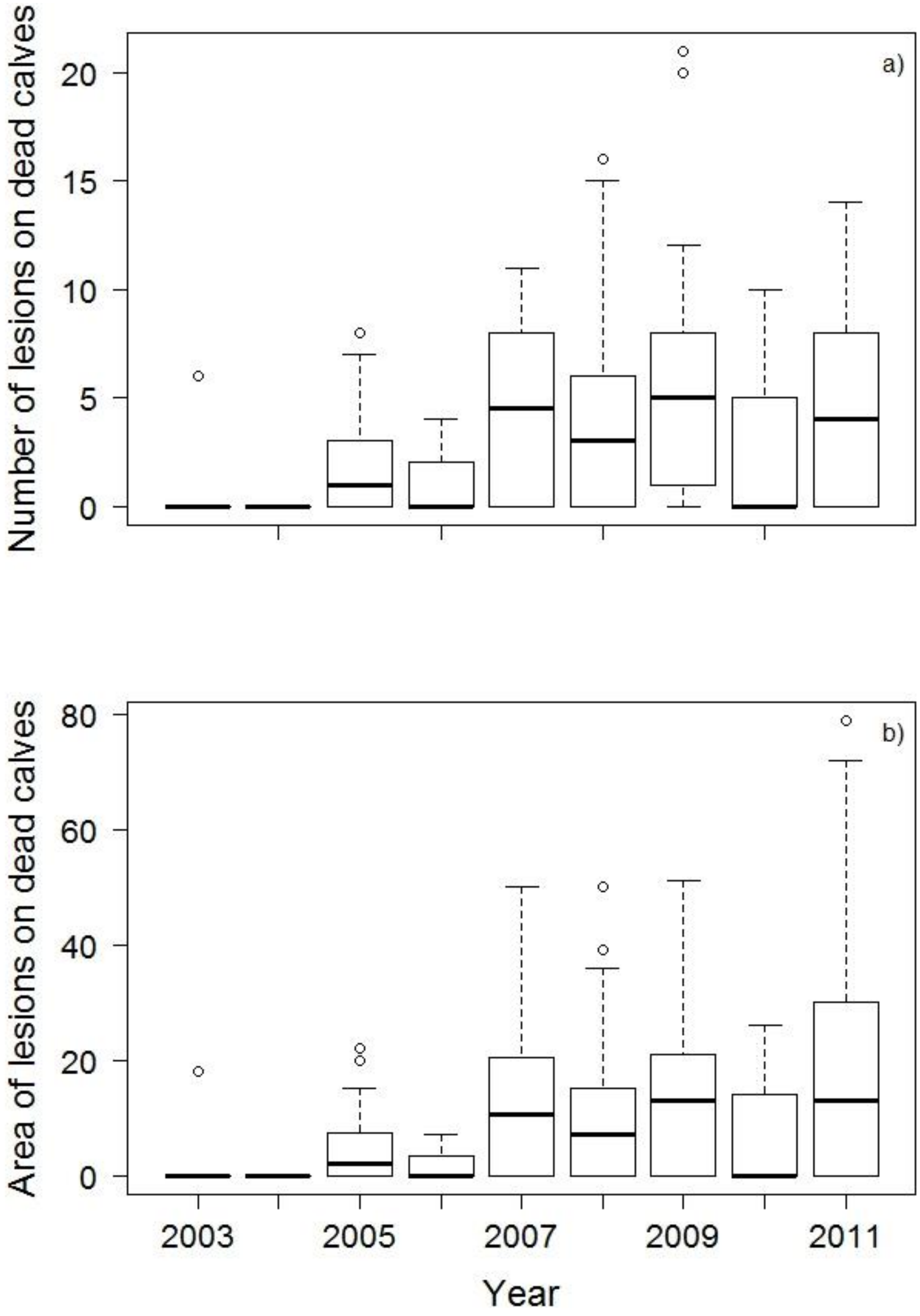


Fig. 4.7. Mean number (a) and area (b) of lesions on dead calves in 2003-2011. Low mortality years: 2004 and 2006, high mortality years: 2003, 2005, 2007-2011.

CHAPTER 5

SHORT- AND LONG-TERM POPULATION CONSEQUENCES OF INCREASED CALF MORTALITY IN THE SOUTHERN RIGHT WHALES OFF ARGENTINA

Abstract

During the last decade, southern right whale (*Eubalaena australis*) calves died in large numbers on their calving ground at Península Valdés, Argentina (606 calf deaths recorded since 2003). The proportion of 2-year calving intervals (which result from calving failures) increased during this period. Normally, females give birth once every three years, spending one year pregnant, one year nursing, and one year recovering to support the next pregnancy. However, females that lose a calf early in lactation may recover quickly and conceive a second calf in one year rather than two; thus the frequencies of 2-year intervals are expected to increase when perinatal (late-term fetus and neonatal calf) mortality increases. Four- and 5-year calving intervals also occur occasionally and are thought to result from calving failures. Using data from annual aerial photographic surveys of the Valdés population, we determined the frequencies of directly observed 2-, 3-, 4- and 5-year intervals that began with a calving in 1971-2009. Two-year intervals constituted 3% of the total in years of relatively low calf mortality (1971-2002, 2004 and 2006), but 16% in years of high calf mortality (2003, 2005 and 2007-2009). A

mathematical model of right-whale population dynamics was used to assess potential short- and longer-term effects of a sustained increase in calf deaths. In this model, the birth rate increases during the first eight years of increased perinatal mortality (roughly equivalent to 2005-13), because a female that loses a calf returns sooner than one that successfully weans a calf. The birth rate begins to decline later, when the female calves that died in high mortality years fail to enter the adult population. If elevated rates of calf mortality continue for another decade or two, the population's growth is expected to slow substantially.

Introduction

Southern right whale (*Eubalaena australis*) populations have been increasing at annual rates of 6-7% for many decades and totaled roughly 12,000 individuals in 2009 (International Whaling Commission [IWC] 2012). However, the population that calves at Península Valdés, Argentina appears to have experienced elevated calf mortality rates in the last decade (Rowntree et al. 2013). From 1971 to 2000, relatively few dead calves were found and their numbers grew at an average rate close to the 6.8% y^{-1} population growth rate estimated for 1971-2000 (Cooke et al. 2003, IWC 2011, Rowntree et al. 2013). Then, the numbers of dead calves increased sharply, totaling 593 in nine of the eleven years between 2003 and 2013 (Fig. 5.1) (Rowntree et al. 2013, Sironi et al. 2014). The cause(s) of this elevated mortality remain unknown (IWC 2011, Thomas et al. 2013, Sironi et al. 2014).

The Valdés right whale population has been studied continuously since 1971 through annual aerial photographic surveys to identify living whales and thereby trace the reproductive histories of individual females (Payne 1986, Payne et al. 1990). During these four decades, a variety of survey efforts have been applied to detect dead whales, ranging from incidental detection during the aerial surveys and reports from local residents in the 1970s and ‘80s, to more frequent air- and land-based surveys focused on detection of dead whales in the 2000s. It is unclear to what extent the recent increase in numbers detected has resulted from increased survey effort, and to what extent it has resulted from a real and possibly severe increase of calf mortality (Rowntree et al. 2013). The reproductive histories of individual female whales, inferred from the annual aerial surveys, can be used to estimate changes in the distribution of calving intervals (times between successive calves). If calf mortality rates really have increased sharply, then the frequencies of abnormal calving intervals also should have increased.

Females in the Valdés population typically give birth to their first calf at around eight years (Cooke 2012) and normally calve once every three years (Whitehead & Payne 1981, Burnell 2001, IWC 2012), as they do in other southern right whale populations (Best et al. 2001, Burnell 2001, IWC 2012) and in the North Atlantic right whale *E. glacialis* (Kraus et al. 2007). During a 3-year interval, mothers spend the first year gestating (Best 1994), the second year lactating (Thomas & Taber 1984, Burnell 2001) and the third year recovering blubber reserves prior to conception in the following year (Fig. 5.2a). However, longer intervals of four and five years are seen at modest frequencies both in southern and in northern right whales (Knowlton et al. 1994, Burnell 2001, Cooke et al. 2003, Best 2005, Kraus et al. 2007, International Whaling Commission 2012) and are interpreted as resulting from calving failures (Knowlton et al. 1994, Burnell 2001).

Four-year intervals may result from: (1) failure to initiate pregnancy in which case the female spends an extra year resting until the following mating season (Fig. 5.2b), or (2) failure to sustain pregnancy in which case the female loses a fetus *early* in gestation and switches to resting until the next mating season (Fig. 5.2c) (Knowlton et al. 1994). Five-year intervals are inferred to result from (3) failure to sustain pregnancy with a fetal loss *late* in gestation, followed by resting until the next mating season (Fig. 5.2d) (Knowlton et al. 1994), or (4) death of a newborn calf followed by resting until the next mating season (i.e., a 3- plus a 2-year interval) (Fig. 5.2e) (Knowlton et al. 1994, Burnell 2001). When a 5-year interval occurs, the mother may be photographed first with a calf that lives and is nursed for a year, second with one born three years later that dies shortly after being photographed, and third with one born just two years later because the mother was able to conceive a year after losing her newborn calf, having been spared the considerable cost in time and energy entailed by a year's lactation (Lockyer 1981). In that case both the 3-year interval and the 2-year interval would have been recorded.

Two-year calving intervals are often missed, however, because they require that the lost calf be photographed during an aerial survey that occurred after it was born but before it died, which will often be a short interval of time. Still, even if most 2-year intervals go unobserved, their *relative* frequencies would be expected to increase following years with higher than average rates of perinatal mortality. Here, we ask: (1) whether 2-year intervals have in fact increased since 2003, coincidentally with the increase in calf mortality at Península Valdés (Rowntree et al. 2013); (2) whether rates of calving success and failure (as estimated from calving intervals) are affected statistically by a mother's age and experience, by the survey year, and by the relative numbers of dead calves seen on the beaches at Valdés; (3) whether the mean age at first parturition has changed during the last four decades; and (4) how the population's growth might be affected if the current high rates of calf mortality were to continue for another decade or more.

Materials and Methods

Calving Interval Distribution

Since 1971 southern right whale individuals at Península Valdés have been photo-identified using the callosity patterns on their heads and pigmentation patterns on their backs (Payne et al. 1983). Photographs of the whales encountered during an aerial survey are compared to known whales in the catalog to find matches or to establish new identities (which are then added to the catalog). Then each identified whale is entered into a database that records its location and any companions including associated calves, which are used to infer the reproductive statuses of females (Payne 1986). We searched the database for females with at least one recorded calving interval (two or more calves) that began with a calving in 1971-2009, and we compiled the frequencies of directly observed 2-, 3-, 4- and 5-year calving intervals. Longer intervals were ignored because their interpretation is ambiguous. Intervals are associated with the year in which they *begin*, not the year they end. The compilation ends with 2009 because 3-year intervals beginning then are completed in 2012, the last year for which we had a complete analysis of the aerial imagery.

Female Age and Age at First Recorded Parturition

Relatively few females are of known age (21%) because callosity patterns are not sufficiently developed in young calves to permit secure identification. Thus to assess the effect of age on rates of reproductive success and failure, we assumed that all females, including those of known age, were eight years old when first seen with a calf (the mean age at first calving estimated by Cooke 2012). However, to compare mean ages at first recorded parturition by decades, we used only the females of known age. These ANOVAs and other analyses described below were conducted in R 3.1.0 (R Core Team 2013).

Female Experience

Females with directly observed 2-, 3-, 4- and 5-year intervals were separated into "inexperienced" (up to three calves) and "experienced" groups (more than three calves recorded) (Elwen & Best 2004), and their relative frequencies of 2-, 3-, 4- and 5-year intervals were compared using chi-square tests with Yates' correction.

Relative Numbers of Dead Calves in High *versus* Low Mortality Years

Rowntree et al. (2013) report the numbers of stranded dead calves per year based on (1) the aerial surveys conducted to identify living whales and reports from local residents for the period 1971-1993; (2) land- and boat-based surveys and reports from an organized stranding network of local residents for the period 1994-2002; and (3) more frequent land- and air-based surveys and reports from an expanded stranding network for the period 2003-2009 (Southern Right Whale Health Monitoring Program, SRWHMP;

Uhart et al. 2008, 2009, Rowntree et al. 2013, Sironi et al. 2014). We define the relative number of dead calves in a year as the number observed, divided by the number of calves estimated to have been born in the Valdés population. Cooke et al. (2001) provide such estimates for 1971-2000; we smoothed those numbers and extrapolated to include 2001-09 by fitting an exponential growth model (Table 5.1). Similar numbers of calves born were estimated by Crespo et al. (2015) using a different dataset.

To distinguish “high mortality” from normal “low mortality” years, we fit an exponential growth model to the numbers of *dead* calves in 1971-2002, assuming an annual growth rate of 6.8% (Cooke et al. 2003) (Fig. 5.1, lower curve). We then defined a hypothetically “augmented” or “corrected” growth model (upper curve) by assuming that the detection efficiency during the years of the SRWHMP (2003-2013) was 1.75 times the average efficiency during 1971-2002. Even under this very generous assumption, the numbers of stranded calves are significantly greater than expected in 2003, 2005 and 2007-13, which are therefore considered “high mortality” years (poisson probabilities, see Fig. 5.1 and Table 5.2).

Comparison of Reproductive Failures and Successes with Female Age, Survey Year, Relative Number of Dead Calves and High v*ersus* Low Mortality Years

We compared the proportions of 2-, 4- and 5-year intervals with 3-year intervals in low and high mortality years using 2x2 contingency tests. We compared the numbers of calving “successes” (3-year intervals) *versus* “failures” (2-, 4- and 5-year intervals) using generalized linear models (glm function, family = binomial) with the following independent variables: high *versus* low mortality years, the reproductive female’s estimated age, survey year, and relative number of dead calves.

Population Growth Model

To assess the potential short- and longer-term effects of an increased calf mortality rate on the growth of the Valdés right whale population, we studied a simplified demographic model of the population. Parameters were based on estimates derived by Cooke et al. (2001, 2003; IWC 2012) from the annual aerial survey data for 1971-2000 (Table 5.3). We varied the parameters of our simplified model to see how the numbers of calves born and the growth of the adult female population would change under four scenarios involving increases in the calf mortality rate.

The four alternative scenarios all share the same set of fixed parameters for the first thirty-four years of the modeled time series, corresponding to 1971-2004 in the annual aerial survey database (i.e., the years prior to 2005 which is the first year with dramatically elevated calf mortality). In the first or “null” scenario, all parameters remain unchanged for the next three decades (2005-2035); in other words, no years of elevated calf mortality occur. In the second scenario, the rate of perinatal calf loss increases from 0.13 to 0.30 in 2005, consistent with the observed increase in calf mortality, but other parameters remain unchanged. In the third scenario, calf loss increases as in the second scenario and in addition, adult and juvenile mortality also increase slowly beginning in 2005 (such that they are 50% larger after twenty years), owing to the stresses induced by increased pregnancy and parturition rates. In the fourth scenario, all the conditions of the third scenario apply and in addition, adult and juvenile mortality rates increase by 30% in

2005, owing to the effects of increased pregnancy and the (unknown) environmental events that are causing increased perinatal calf mortality.

Results

Increase of Two-Year Calving Intervals in High Mortality Years

We found 408 southern right whale females with at least one calving interval in the photo-ID database. Two-year intervals were 2% of the total in the 1970s, 3% in the 1980s, 2% in the 1990s, and 11% in the 2000s (a fivefold increase).

Reproductive failures were indicated more frequently (from the calving-interval data) in high mortality years with unusually large numbers of stranded calves on the beaches (when 31% of intervals were not 3-year) than in normal low mortality years (20% not 3-year) ($p = 0.008$). Table 5.4 shows the numbers of 2-, 3-, 4- and 5-year intervals separately for both kinds of years, and Fig. 5.3 shows the numbers of 2- and 3-year intervals separately for all years. Two-year intervals began vastly more often in high mortality years (15.7% of the high mortality total) than in low mortality years (3% of the low mortality total) ($p < 0.001$), but 4- and 5-year intervals showed no significant or notable differences ($p \geq 0.15$).

No individual female showed more than one 2-year interval (18 different females in high mortality years, 20 in low mortality years, 38 in all). Their ages at the beginnings of the 2-year intervals ranged from eight to 29 years, and their cumulative numbers of known calves ranged from two to eight.

Reproductive Failures Do Not Depend on Female Age, Experience, or Survey Year

The relative probabilities of reproductive success (3-year intervals) and failure (2-, 4- and 5-year intervals) did not depend on a mother's estimated age ($p = 0.8$) or the survey year ($p = 0.6$). Female experience (three or fewer known calves *versus* four or more) also had no detectable effect on the probabilities of success and failure (2-year intervals: $X^2 = 0.01$, $p = 0.91$; 4-year intervals: $X^2 = 0.06$, $p = 0.81$; 5-year-intervals: $X^2 = 0.95$, $p = 0.6$) (Table 5.5).

Reproductive Failures Increase with the Relative Numbers of Dead Calves

The proportion of all calving failures (2-, 4- and 5-year intervals), considered together, were correlated with the relative numbers of dead calves on the beaches ($p = 0.05$). Considering the nonstandard intervals separately, 2-year intervals were highly significantly correlated with the relative numbers of dead calves ($p < 0.001$), but the proportions of 4- and 5-year intervals were not ($p = 0.8$ and $p = 0.97$, respectively).

Age at First Parturition Does Not Change over Decades

The mean age at first recorded parturition was 11.7 ± 4.9 years with a range of six to thirty-three years. The decadal means did not differ significantly ($p = 0.5$).

Delayed Reduction of Population Growth Rate

The adult female population continues to grow following the onset of increased calf mortality, but it does so at substantially different rates under the four modeled scenarios (Fig. 5.4). Under the first or “null” scenario, the rate of increase is 6.5% yr^{-1}, as assumed. This null expectation (case *a*) is represented in Fig. 5.4 by thin horizontal lines at elevations of 1.0 (for adult females) and 0.307 (for calves). From 2005 to 2015, under each of the other scenarios (cases *b-d*, heavier lines), the adult female populations continue to increase at nearly the same rate, even though calf mortality has increased sharply. Counter-intuitively, both the absolute and relative numbers of calves born *increase* slightly, relative to the null expectation. Then from 2015 to 2025, the rate of population growth visibly slows, relative to expectation. By the end of 2025, the growth rates approach their new steady-state values under the parameters of each scenario (5.6%/yr for scenario *b*, 4.2% for scenario *c*, 3.6% for scenario *d*). At this time the total population sizes are 12%, 20% and 28% smaller than under the null scenario, and by 2035 the shortfalls are 19%, 34% and 44% (Fig. 5.4).

Discussion

The normal calving interval for right whales is three years (Whitehead & Payne 1981, Knowlton et al. 1994, Best et al. 2001, Burnell 2001, Cooke et al. 2001, 2003, Kraus et al. 2007, IWC 2012). Two-year intervals are interpreted as the second phase of what is more often seen as a 5-year interval, when a calf is recorded shortly after birth but then dies and the mother becomes pregnant the following year. Thus an apparent 5-year interval may often be a 3-year interval, not recorded, which is followed by a 2-year interval. The analyses reported here show that years when elevated numbers of dead calves are detected on the beaches at Península Valdés are also years when elevated numbers of 2-year calving intervals begin. This finding supports the standard interpretation of 2-year intervals and implies that the recent increase in calf strandings is caused mainly by increased calf mortality, not by increased detection efficiency.

Two-year intervals began much more often in the high mortality years of 2003, 2005 and 2007-09 (15.7% of all intervals, see Table 5.4) than in typical low mortality years (3.0%). Taken at face value, this difference would imply that the calf mortality rate was 15.7/3.0 = 5.2 times higher in those five high mortality years than in typical years, on average, which is a larger difference than suggested by Fig. 5.1 and Table 5.2. During those five years, 67.9 stranded calves were expected but 303 were found, which is 4.5 times more than the growth-adjusted expectation based on typical years. The lower 95% confidence limit for the proportion of 2-year intervals in high mortality years is 13.9% (Jeffreys bayesian estimate), and the upper c.l. for typical years is 4.5%, so the actual ratio of perinatal mortality rates in the two sets of years could conceivably be as small as 3 or 4. Thus given the inherent statistical uncertainties, the evidence from calving intervals is fully consistent with the evidence from stranded calves; both of these completely independent sources of data indicate that perinatal calf mortality rates increased several fold (probably 4-6x, on average) during the high mortality years that began in 2003.

Cooke (IWC 2012) also found an increase in the estimated proportion of 2-year intervals at Península Valdés during the 2000s, by fitting a highly parameterized demographic model to the photo-ID database (Cooke et al. 2003). The best fit indicated, in addition, that 4- and 5-year intervals also increased in frequency, which was not seen in our analysis of directly observed intervals.

Four-year intervals would not be expected to increase with calf mortality, because they are thought to result from failures to *initiate* or *sustain* pregnancy (Fig. 5.2b and c). However, if apparent 5-year intervals often result from unrecorded 2-year intervals due to failures *during* lactation (Fig. 5.2e), then they might be expected to increase in parallel with recorded 2-year intervals, and with increased numbers of stranded calves. One possible explanation for our failure to find an increase of 5-year intervals is that some of them may result from failures to *complete* pregnancy (Fig. 5.2d) due to food limitation in the whales' feeding grounds. For example, Leaper et al. (2006) found an increase in the occurrence of 5-year intervals in the Valdés population following El Niño years when prey (Antarctic krill, *Euphausia superba*) abundance declined (IWC 2011); a remarkable number of 5-year intervals (10) began in 1979, consistent with the hypothesis that many females failed to complete their pregnancies in 1982, when krill were very scarce (Fig. 5.2d, Table 5.6). During the early 1980s, however, we did not record a significant increase in the number of stranded calves at Valdés (Fig. 5.1) or an increase in the occurrence of 2-year calving intervals (Table 5.6), suggesting that mothers may have lost their calves *before* arriving at the Valdés calving ground. Food limitation has also been suggested as a potential cause of the increase in 5-year intervals that occurred in North Atlantic right whales during the 1990s (IWC 2001, Kraus et al. 2007).

Our failure to find more 5-year intervals during the period of elevated calf mortality also might be caused, at least in part, by statistical uncertainty. The upper confidence limit on the proportion of 5-year intervals during high mortality years is

15.9%, while the lower limit on the proportion during low mortality years is 8.2% (or 6.8% if we exclude the 10 anomalous intervals from 1979). Thus our data do not rule out the possibility that 5-year intervals did increase during high mortality years, despite what we saw, which weakly indicates the opposite.

Finally, it is possible that 2-year intervals have been detected more efficiently during high mortality than low mortality years. Calves stranded in high mortality years are longer, on average, than those stranded in low mortality years, which suggests that they were older when they died (Rowntree et al. 2013). In that case each of them would have been more likely to be photographed during an aerial survey, and we would overestimate the frequency of 2-year intervals in high mortality years relative to their frequency in low mortality years (consistent with the larger increase of 2-year intervals than of stranded calves, as discussed above); and as a consequence, we would also underestimate the frequency of 5-year intervals.

Two-year calving intervals are rarely observed in other right whale populations. In southern right whales off Australia, Brazil and South Africa, 2-year calving intervals represent around 2.5% to 5% of the total 2-, 3-, 4- and 5-year intervals recorded (Bannister 1990, Best 2005, Groch et al. 2005). These percentages are similar to the steady 2-3% occurrence of 2-year intervals that we estimate for the Valdés population in the 1970s, ‘80s and ‘90s, but very different from the 13% recorded in the 2000s. Two-year calving intervals are also rare in northern right whales (Knowlton et al. 1994), representing just 1.9% of all the intervals recorded over a 25-year period (Kraus et al. 2007).

Each of the 2-year intervals we detected was experienced by a different mother, so there is no evidence to suggest that some individuals are especially susceptible to the environmental factor(s) causing increased calf mortality. There is also no association with the mother's age or known calving experience. Many kinds of reproductive failure are expected to increase as female mammals approach the age of reproductive senescence (Packer et al. 1998), although the evidence appears to be inconclusive for cetaceans (Marsh & Kasuya 1986, Tarpley et al. 1998). Elwen and Best (2004) found that 2- and 4-year intervals *decreased* with female experience in the southern right whales off South Africa; mothers with three or fewer known calves had more unsuccessful calving intervals than mothers with more than three calves.

The mean age at first recorded parturition did not change over four decades for the Valdés population. Declines in the mean age of sexual maturity appear to have occurred in fin whales (*Balaenoptera physalus*) in response to intense exploitation. Females reached sexual maturity at ten or eleven years in 1910-1920, but later in the 20th century they often reached sexual maturity at six years of age, possibly as a consequence of reduced population size (Lockyer 1972).

The growth rate of the Valdés population may be slowing. Cooke (IWC 2012) obtained a lower estimate of the growth rate for 2001-2010 (5.1% yr^{-1}) than for 1971-2000 (6.8% yr^{-1}) from a fit of his demographic model to the aerial survey data through 2010. Also, as was mentioned above, this fit also estimated that the frequencies of non-3-year intervals (i.e., calving failures) had increased in the 2000s.

Somewhat paradoxically, the numbers of calves born at the Península also appear to have increased substantially during this period. Crespo et al. (2014, 2015) counted all individuals visible in a strip extending from the beach to approximately 2 km offshore in aerial surveys conducted repeatedly throughout the seasons of 1999-2014. The apparent rate of increase for calves was higher, on average, than for other age and status classes (mother-calf pairs, mating groups and solitary whales). The simplified demographic model described here (Fig. 5.4) shows that an apparent increase of calf production is expected, initially, if the rate of perinatal calf mortality increases, because more females return in two rather than three years; more calves are born, but fewer of them are recruited, later, into the adult female population. Thus a *depression* of the underlying growth rate of the *population* (as estimated by Cooke's model IWC 2012) is consistent with an actual short-term *elevation* of the growth rate of *births*.

Our model suggests that if high calf mortality rates continue into the future, then the Valdés population's growth rate will be substantially depressed. Under the null scenario (high calf mortality rate does not occur), the population will increase at around 6.5%/yr, as it has done on average for decades (Cooke et al. 2001, 2003) (Fig. 5.4a) and the number of calves born will remain steady through time. However, under the three scenarios where a high calf mortality rate continues, both the population growth rate and the number of calves born will decrease (Fig. 5.4b, 5.4c and 5.4d). This decrease is expected to become evident only about a decade after the onset of increased calf mortality rates (i.e., beginning around 2015).

In the first decade of the mortality crisis (2005-2015), under these three scenarios, the adult female population will continue to grow because females born before the high mortality years continue to enter the reproductive population. In the second and third decades (2015-2035) the growth rate decreases because fewer females born during high mortality years survive to enter the reproductive population. In addition, fewer calves are produced because fewer mothers are recruited from high mortality years. Thus the short-term effects of increased calf mortality are slight, but the longer-term effects could be substantial.

Population growth rates decrease substantially under the third and fourth scenarios because juvenile and adult mortality rates increase. Gestation and especially lactation are costly processes for mammals, particularly for capital breeders such as baleen whales that fast while lactating (Oftedal 2000, Miller et al. 2012). Survival could become problematic when whales do not meet the energy demands of reproduction, migration and self-maintenance. Adult female survival could be compromised when mothers repeatedly invest more energy in migrating sooner to the calving ground and calving (unsuccessfully) at shorter intervals.

In summary, juvenile females that were born prior to 2005 (when the period of sustained high calf mortality rates began) have now moved into the breeding population. The recruits entering adulthood in coming years will be from post-2005 cohorts that were depleted by high rates of calf mortality. In addition, small reductions in the survival of juveniles and adults might further reduce the growth rate. Thus work to estimate juvenile and adult mortality rates may be just as important as work to estimate the rates of calf mortality, although the most urgent need is to identify the still unknown cause(s) of the ongoing period of increased calf mortality.

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Table 5.1. Number of calves estimated to be born in the Valdés right whale population. Estimated fit is the number of calvings estimated by Cooke et al. (2001). Smoothed fit is an extrapolation of the estimated fit. We assume r = 0.068 and estimated n0(1970) = 26.4. "Average" is the cumulative mean difference between the estimated calf production and the smoothed fit.

Year	**Estimated fit**	**Smoothed fit**	**Difference**	**Average**
1971	28	28.3	-0.3	-0.26
1972	34	30.2	3.8	1.75
1973	42	32.4	9.6	4.37
1974	36	34.7	1.3	3.62
1975	40	37.1	2.9	3.48
1976	47	39.7	7.3	4.11
1977	37	42.5	-5.5	2.74
1978	43	45.5	-2.5	2.09
1979	64	48.7	15.3	3.56
1980	41	52.1	-11.1	2.09
1981	36	55.8	-19.8	0.1
1982	55	59.7	-4.7	-0.3
1983	63	63.9	-0.9	-0.34
1984	73	68.4	4.6	0.01
1985	77	73.2	3.8	0.26
1986	69	78.4	-9.4	-0.34
1987	88	83.9	4.1	-0.08
1988	101	89.8	11.2	0.55
1989	96	96.1	-0.1	0.52
1990	107	102.9	4.1	0.7
1991	102	110.1	-8.1	0.28
1992	115	117.8	-2.8	0.14
1993	147	126.1	20.9	1.04
1994	133	135	-2	0.91
1995	142	144.5	-2.5	0.77
1996	172	154.7	17.3	1.41
1997	163	165.6	-2.6	1.26
1998	151	177.2	-26.2	0.28
1999	187	189.7	-2.7	0.18
2000	212	203	9	0.47
2001		217.3		
2002		232.6		
2003		249		
2004		266.5		
2005		285.2		
2006		305.3		
2007		326.8		
2008		349.8		
2009		374.4		

Table 5.2. Observed and predicted (Pred) number of dead calves. We assume a population growth rate of 0.068. “Observed” indicates the number of dead calves recorded at Valdés in 1971-2013. “Pred(71-02)” indicates predicted number of dead calves after fitting a curve to the numbers observed in 1971-2002. “Pred*1.75%” indicates predicted number of dead calves assuming the SRWHMP increases detection efficiency by 75%. The best-fit intercept for the Pred(71-02) curve is 1.13 calves. “<” indicates significantly *too few* strandings, “>” = *too many*.

Year	**Observed**	**Pred(71-02)**	**Pred*1.75%**	**P(obs|175%)**	
1971	2	1.2 (-0.8)	2.1 (0.1)	0.65	
1972	1	1.3 (0.3)	2.3 (1.3)	0.34	
1973	1	1.4 (0.4)	2.4 (1.4)	0.30	
1974	0	1.5 (1.5)	2.6 (2.6)	0.07	
1975	0	1.6 (1.6)	2.8 (2.8)	0.06	
1976	0	1.7 (1.7)	3.0 (3.0)	0.05	
1977	1	1.8 (0.8)	3.2 (2.2)	0.17	
1978	2	1.9 (-0.1)	3.4 (1.4)	0.34	
1979	0	2.1 (2.1)	3.6 (3.6)	0.03	<
1980	0	2.2 (2.2)	3.9 (3.9)	0.02	<
1981	2	2.4 (0.4)	4.2 (2.2)	0.21	
1982	3	2.6 (-0.4)	4.5 (1.5)	0.35	
1983	1	2.7 (1.7)	4.8 (3.8)	0.05	<
1984	2	2.9 (0.9)	5.1 (3.1)	0.11	
1985	6	3.1 (-2.9)	5.5 (-0.5)	0.47	
1986	3	3.4 (0.4)	5.9 (2.9)	0.16	
1987	5	3.6 (-1.4)	6.3 (1.3)	0.40	
1988	5	3.8 (-1.2)	6.7 (1.7)	0.34	
1989	0	4.1 (4.1)	7.2 (7.2)	0.0007	<
1990	0	4.4 (4.4)	7.7 (7.7)	0.0005	<
1991	6	4.7 (-1.3)	8.2 (2.2)	0.28	
1992	0	5.0 (5.0)	8.8 (8.8)	0.0001	<
1993	2	5.4 (3.4)	9.4 (7.4)	0.004	<
1994	8	5.8 (-2.2)	10.1 (2.1)	0.32	
1995	9	6.2 (-2.8)	10.8 (1.8)	0.36	
1996	4	6.6 (2.6)	11.6 (7.6)	0.01	<
1997	4	7.1 (3.1)	12.4 (8.4)	0.005	<
1998	11	7.6 (-3.4)	13.3 (2.3)	0.33	
1999	10	8.1 (-1.9)	14.2 (4.2)	0.16	
2000	14	8.7 (-5.3)	15.2 (1.2)	0.44	
2001	10	9.3 (-0.7)	16.3 (6.3)	0.07	
2002	10	10.0 (-0.0)	17.4 (7.4)	0.04	<
2003	29	10.7 (-18.3)	18.6 (-10.4)	0.02	>
2004	13	11.4 (-1.6)	20.0 (7.0)	0.07	
2005	36	12.2 (-23.8)	21.4 (-14.6)	0.002	>
2006	16	13.1 (-2.9)	22.9 (6.9)	0.09	
2007	77	14.0 (-63.0)	24.5 (-52.5)	0	>
2008	89	15.0 (-74.0)	26.2 (-62.8)	0	>
2009	72	16.0 (-56.0)	28.0 (-44.0)	0	>
2010	40	17.2 (-22.8)	30.0 (-10.0)	0.05	>
2011	58	18.4 (-39.6)	32.1 (-25.9)	$2.56\text{x}10^{-05}$	>
2012	112	19.7 (-92.3)	34.4 (-77.6)	0	>
2013	64	21.0 (-43.0)	36.8 (-27.2)	$3.06\text{x}10^{-05}$	>

Table 5.3. Estimated parameters used in the population quantitative model to assess the potential short- and longer-term effects of an increased calf mortality rate on the growth of the Península Valdés right whale population.

Parameter	**Estimated probability**	**References**
3-year calving interval	0.74	Cooke et al. 2001, 2003
4-year calving interval	0.09	Cooke et al. 2001, 2003
5-year calving interval	0.13	Cooke et al. 2001, 2003
Birth sex ratio	0.5	Tormosov et al. 1998
Yearly adult female survival	0.98	Cooke et al. 2003
Weaned female calves (juveniles entering their 2nd year) that survive to enter the resting cohort at age 8	0.92	Cooke et al. 2001
Equilibrium annual growth	0.065	This study

Table 5.4. Observed calving intervals (“successful”: 3-years; “failures”: 2-, 4- and 5-year years) of the southern right whales at Península Valdés, Argentina for the period 1971-2009. [a]“Low mortality” years are defined as years where the observed mortality rate was similar to the expected rate (1971-2002, 2004 and 2006) (see Fig. 5.1). [b]“High mortality” years are defined as years where the observed mortality rate was higher than the expected rate (2003, 2005 and 2007-2009) (see Fig. 5.1).

Calving interval	**Low mortality years**[a]		**High mortality years**[b]	
2-year	20	3.0%	18	15.7%
3-year	536	79.9%	79	68.7%
4-year	46	6.9%	7	6.1%
5-year	69	10.3%	11	9.6%
Total	671	100%	115	100%

Table 5.5. Observed calving intervals in inexperienced and experienced southern right whale females at Península Valdés, Argentina for the period 1971-2009.“Inexperienced females” are females with up to three calves observed. “Experienced females” years are females with more than three calves observed.

Calving interval	**Inexperienced females**	**Experienced females**
2-year	30	8
3-year	472	143
4-year	42	11
5-year	58	22
Total	602	184

Table 5.6. Number of observed calving intervals beginning in 1971-2009. High mortality years are marked "high" in the last column.

Year	**Calving intervals**				**Mortality**
	2-year	**3-year**	**4-year**	**5-year**	**year**
1971		5	1		
1972		16	3		
1973	1	18	3		
1974		4	1	2	
1975		10	2	1	
1976		13	1	1	
1977	1	6		4	
1978		9		4	
1979		5	3	10	
1980		6		1	
1981		6	1		
1982		9		1	
1983	1	14	3	4	
1984	1	25	2	3	
1985		17		1	
1986	2	16	2		
1987		44	1	2	
1988	1	15	1	2	
1989	1	11	2	2	
1990		33	2	1	
1991		16		1	
1992	1	9	3		
1993		28		2	
1994		14	2	3	
1995		9	1	3	
1996	1	35		3	
1997	2	12	1	1	
1998	1	17	1	2	
1999	1	33	4	6	
2000	2	23	1		
2001	2	10	1	4	
2002	1	23	1	1	
2003	4	18	1		high
2004	1	11	2	3	
2005	6	20	2	5	high
2006		14	1	1	
2007	3	7	2	6	high
2008	3	11	2		high
2009	2	23			high
Total	38	615	53	80	

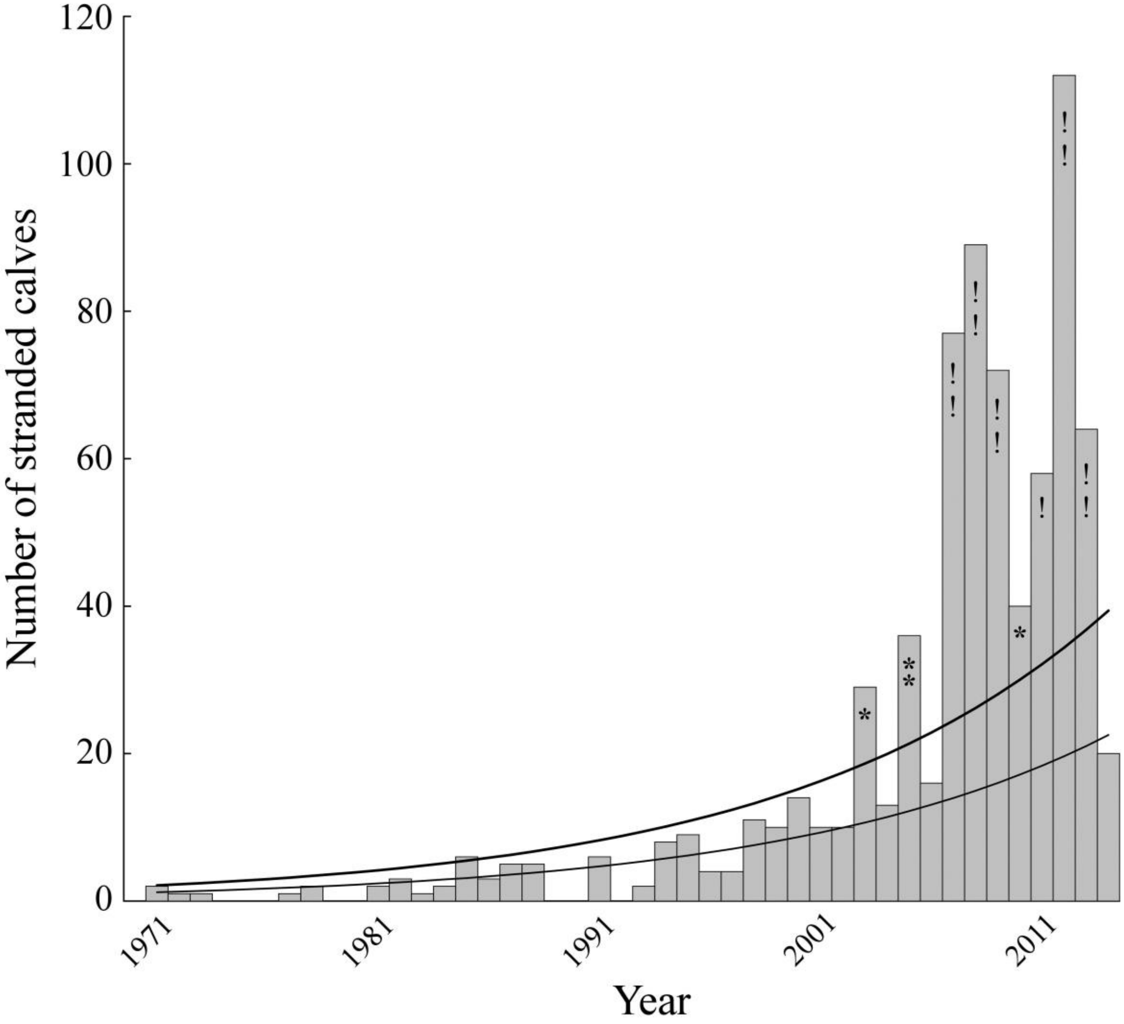

Fig. 5.1. Numbers of stranded calves recorded at Península Valdés, 1971-2013. The lower curve (thinner line) is an exponential fit to the data for 1971-2002, assuming a 6.8% yearly rate of increase. The upper curve (heavier line) shows the numbers that would be expected, on average, if the detection efficiency were 1.75 times the average efficiency during 1971-2002. Even on this generous assumption about the improvement in detection that might have resulted from initiation of the SRWHMP, calf deaths in 2003, 2005 and 2007-13 are all significantly greater than the expectations (binomial probabilities: *, **, ! and !! indicate significance levels of $p < 0.05$, 0.01, 0.0001 and 0.00000001, respectively). Calf deaths in 2004 and 2006 are close to the fit for 1971-2002 and well below the "greatly-improved-detection" curve, but not significantly so ($0.05 < p < 0.1$ in both cases).

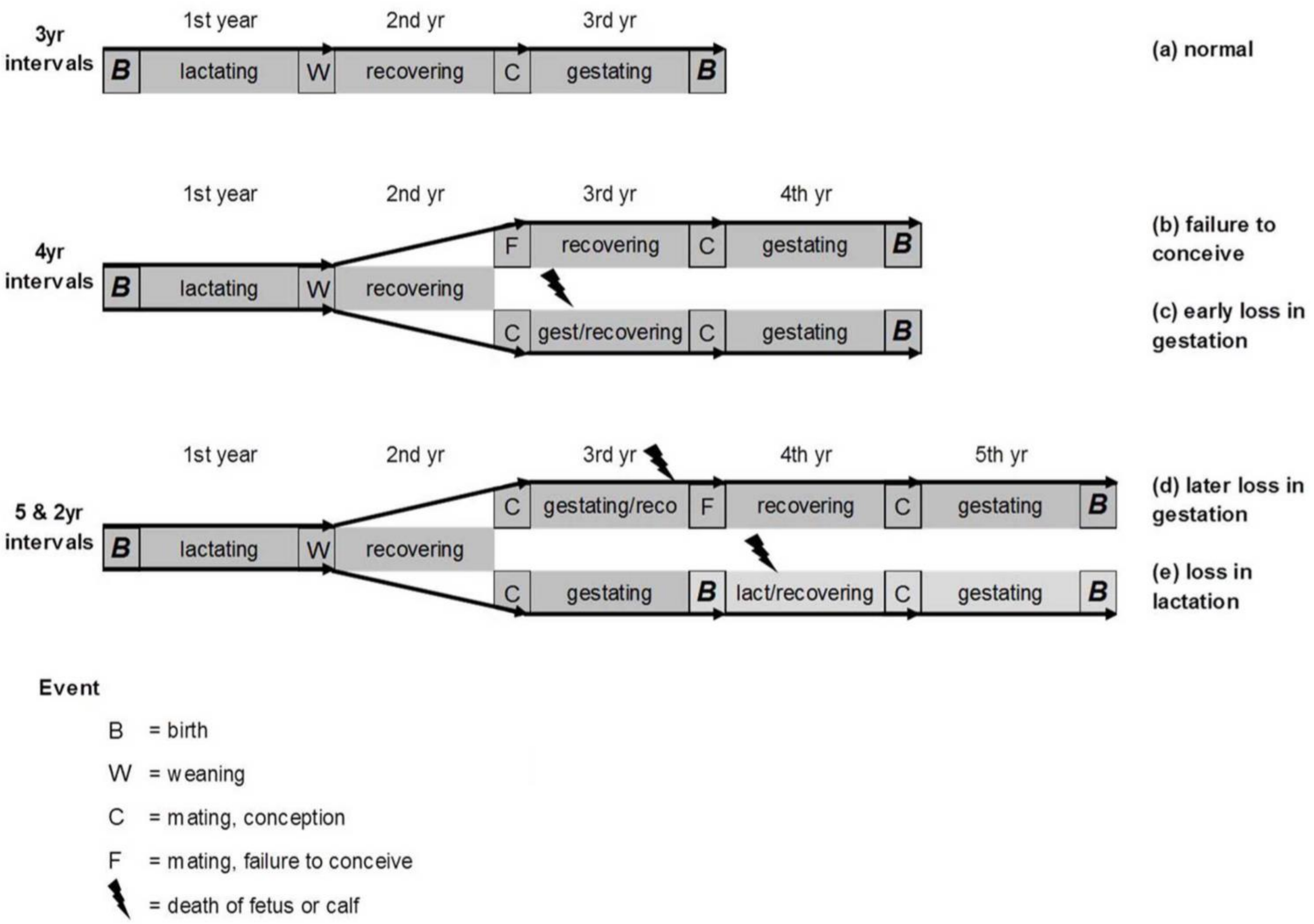

Fig. 5.2. Five potential scenarios for explaining normal (3-year) and abnormal (2-, 4- and 5-year) calving intervals in the right whale species. The lightning bolt symbol indicates fetus or calf loss. Years are indicated on top of each scenario. (a) 3-year calving interval or normal. (b) 4-year interval with an extra recovering year. (c) 4-year interval with fetus loss. (d) 5-year interval with two extra recovering years. (e) 5-year interval with calf loss. Abbreviations: birth (B), weaning (W), conception (C), failure to conceive (F).

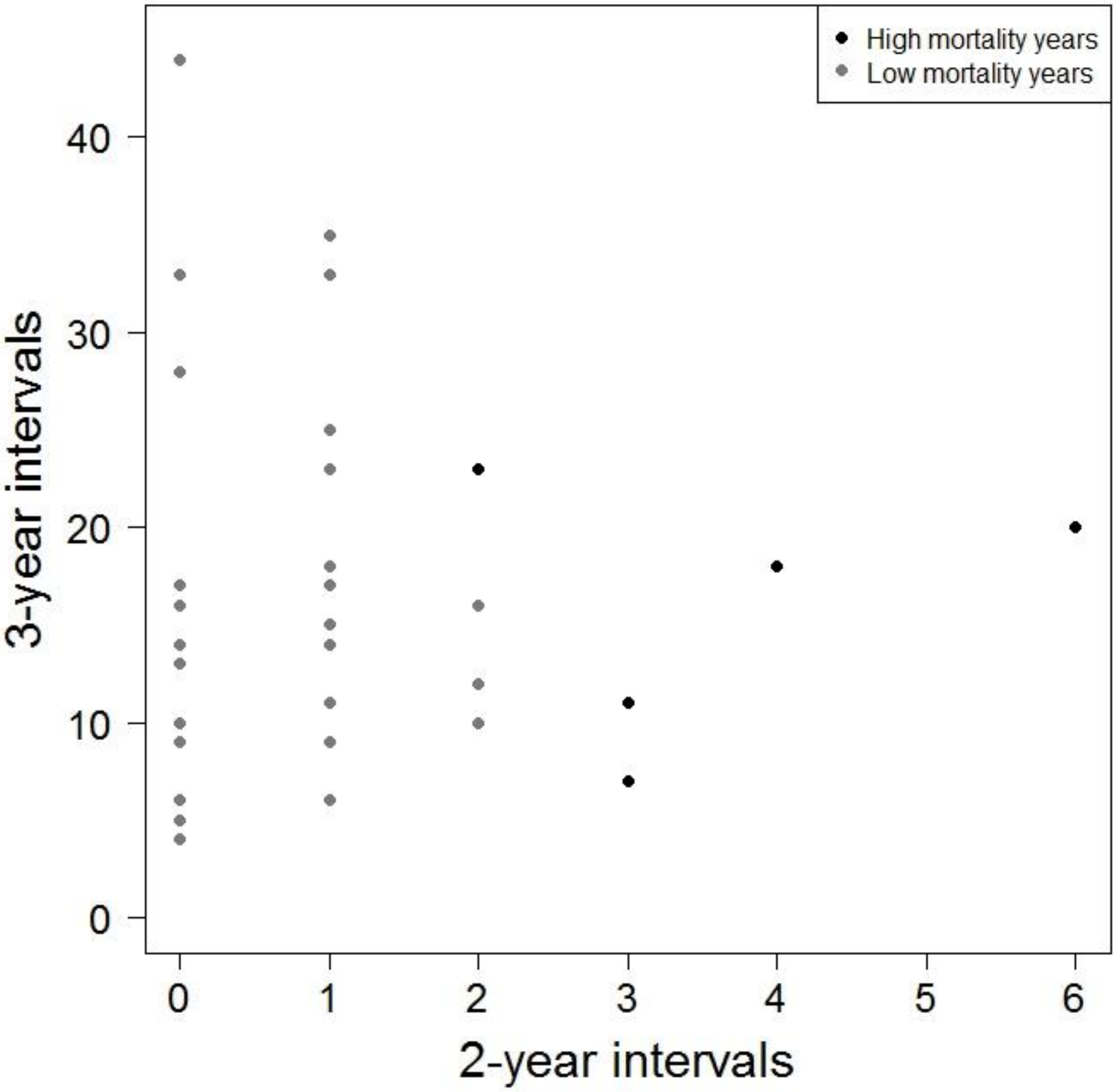

Fig. 5.3. Number of 3-year and 2-year calving intervals per year (1971-2008). Black dots indicate high mortality years (2003, 2005 and 2007-09) and grey dots (1971-2002, 2004 and 2006) indicate low mortality years.

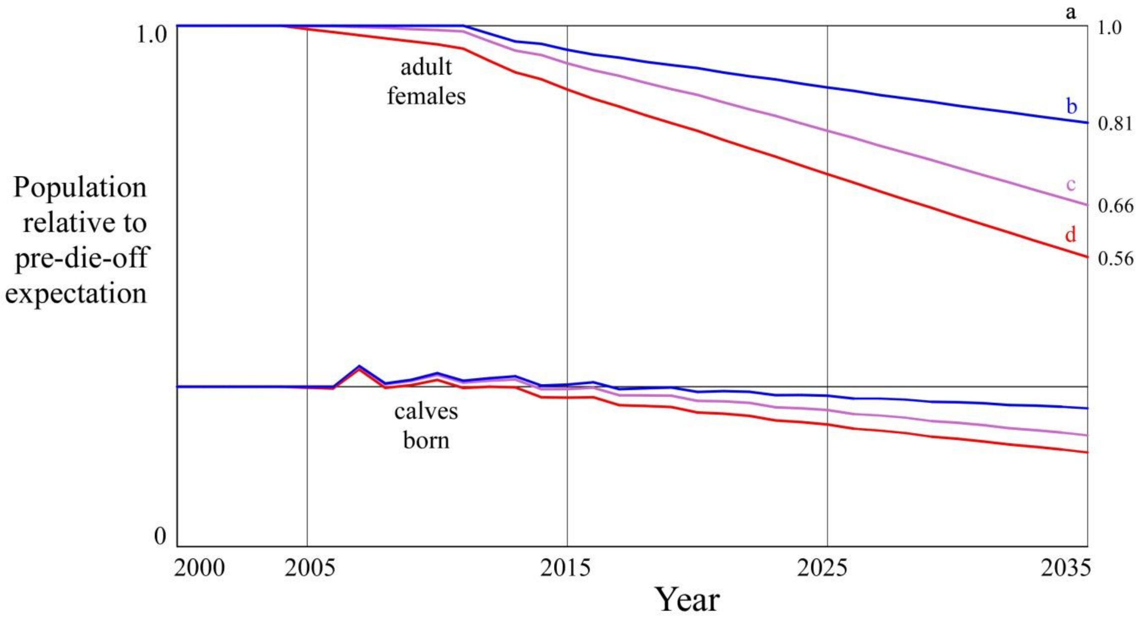

Fig. 5.4. Relative female population sizes by year under four scenarios. Trajectories are shown separately for adult females and calves, normalized by the population size expected under the null scenario that no high mortality years occur (scenario “a”, horizontal black lines). Under scenario “b” (blue lines), perinatal calf mortality permanently changes from 0.13 to 0.3 in year 2005. Under scenario “c” (purple lines), the adult and juvenile mortality rates also begin a linear increase in 2005, such that they are 50% larger after 20 years. Under scenario “d” (red lines), these mortality rates also jump by 30% in 2005. The population continues to grow under all of these scenarios, but at substantially reduced rates (*e.g.*, under scenario “d” at only about half of its original rate). The population’s relative sizes 30 years after the onset of the high mortality years are indicated numerically on the right. Numbers at the ends of the adult female trajectories indicate relative population sizes. Initial parameters are close to those estimated as averages for the period 1971-2000 by Cooke et al. (2001, 2003), except that 2-year calving intervals are assumed never to be successful (i.e., the prior calf is always lost). The sex ratio at birth is assumed to be 0.5, yearly female survival is 0.98, and weaned female calves (juveniles entering their second year) survive to enter the resting cohort at age 8 with probability 0.92. Under these assumptions the equilibrium annual growth increment is 0.