Mortalities of right whales (*Eubalaena australis*) at Peninsula Valdes between 1971 and 2010: recent increases and their possible causes

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ABSTRACT

Hundreds of southern right whales (*Eubalaena australis)* died on their nursery ground at Península Valdés (PV), Argentina from 2003 through 2009. Over 368 dead whales were recorded, with peaks of mortality in 2005 (47), 2007 (83), 2008 (96) and 2009 (79). Calves in their first three months of life were most affected by the mortality (90%). The timing of the unusual mortalities differed between years with significantly more deaths occurring early in the nursery season in 2008 and 2009 and late in the season in 2005 and 2007. Calves that died late in the season in 2005 and 2007 were much larger than newborns, indicating that they had grown at normal rates before dying. Their growth implies that they were probably healthy before death and succumbed to some sudden cause of death. In contrast, in 2008 and 2009 the cause is most plausibly some kind of population-wide effect (such as nutritional stress) that was experienced by all females regardless of age, size and experience causing calves to die shortly after birth. While many samples and much information have been gathered to date, common significant lesions or pathologic processes to explain the yearly or recurrent mortalities have not been identified. Ongoing monitoring for independent, multifactorial/interrelated or concurrent disease processes, including infectious, toxic or nutritional disease, genetic or environmental factors including food availability and maternal and calf fitness are critical for establishing the cause(s) of the recent recurrent, significant mortality of young right whales at Península Valdés.

INTRODUCTION

Three hundred and sixty-eight southern right whales (*Eubalaena australis)* died on their nursery ground at Península Valdés (PV), Argentina (Fig 1) from 2003 through 2009 with peaks of mortality in 2005 (47), 2007 (83), 2008 (96) and 2009 (79). Most of the dead animals (90%) were calves in their first three months of life (Table 1, Fig 2). An International Whaling

Commission workshop convened in March 2010 to review available information about these unusual mortality events identified three possible causes needing further study: (i) decreased availability of food, (ii) exposure to biotoxins, and (iii) infectious disease (IWC 2010 Document SC/62/Rep 1).

Unlike toothed whales, baleen whales rarely die in large numbers. The first known report of a 'multiple-death event' (other than incidents involving ice entrapment) occurred in 1987 when 14 humpback whales (*Megaptera novaeangliae*) died in Cape Cod Bay (Massachusetts, USA) after consuming saxitoxin-contaminated mackerel (*Scomber scombrus*) (Geraci *et al.* 1989). In early 1995, at least 425 marine mammals, including individuals from three species of baleen whales, and 200 seabirds were found dead in the upper Gulf of California, Mexico (Vidal 1996). Four Bryde's whales (*Balaenoptera edeni*) were found dead in the Persian Gulf in 2007 (Braulik *et al.* 2010) but no details were available regarding the cause(s) of those deaths. Evidence of another possible 'die-off' in the upper Gulf of California includes the finding of the remains of 10 dead baleen whales there in April 2009 (J. Urbán-Ramírez, pers. comm. to Brownell). Also, about 50 humpback whales were found dead along the coast of Western Australia during the latter half of 2009 (Doug Coughran, pers. comm. to Brownell). Ninty-six dead humpback whales (60% calves) were found off Brazil in 2010, more than triple the annual mean of dead humpback whales found from 2002-2009 (pers. comm. M. Marcondes). The largest reported baleen whale 'die-off' involved gray whales (*Eschrichtius robustus)* in the eastern North Pacific. In 1999 and 2000, respectively, 283 and 368 gray whale deaths were documented. The majority of dead gray whales were adults and juveniles (only 7% were calves) (Gulland *et al.* 2005; Brownell *et al.* 2007).

Nineteenth century whaling decimated right whale populations around the world. Consequently, the northern hemisphere species are endangered with fewer than 300 North Pacific right whales (*Eubalaena japonica*)(Wade *et al.* 2011) and 500 North Atlantic right whales (*Eubalaena glacialis*)(Pettis 2009). In contrast, the southern hemisphere right whales (*Eubalaena australis)* are faring better with all populations recovering and growing at rates of 7-8% per year (IWC 2001), with the exception of the Chile-Peru population which is considered highly endangered. Southern right whales give birth and nurse their calves off the eastern coast of South America, Southern Africa, Australia and New Zealand. The southern right whale population that uses Península Valdés (PV), Argentina as a nursery ground has been studied continuously since 1971 using aerial photographic surveys of the entire 495 km perimeter of the coast to record the individuals present each year, their locations and the presence of calves (Payne et al. 1983, Payne, 1986). As of 2008, the catalogue contained over 2,600 known individuals. The PV population grew at a rate of 6.8% yr^{-1} (SE 0.5%) through the year 2000 (Cooke et al. 2003) when its population was estimated to have 3,346 whales.

Calves are born in the protected gulfs of PV (Fig. 1) (Whitehead & Payne 1981; Payne, 1986) and spend their first months of life there (Thomas & Taber 1984). The nursery season extends from May through December, with peak numbers present in late September-early October (Payne 1986). Most births occur in or near August although newborns are also seen as late as October (Whitehead & Payne 1981). Females reach reproductive maturity at 9 years of age (mean 9.1, SE 0.11 yr), and usually calve once every three years (X^2 3.4, SD ± 0.4 yr) (Cooke *et al.* 2001, Cooke *et al.* 2003). The normal reproductive cycle includes one year in gestation (Best 1994), one year in lactation and one year resting while regaining energy reserves to support another pregnancy (Knowlton *et al.* 1994). Apparent calving intervals of two, four and five years are thought to result from calving failures (Knowlton *et al.* 1994). Adult whales are primarily fasting during the 2-3 months they are on the nursery ground, but begin to feed sporadically in late September or early October on spring plankton blooms (Payne 1995, Sironi 2004, Hoffmeyer et al. 2010). The mean length at birth for southern right whales is estimated to be 5.5 - 6.1 m (Whitehead & Payne 1981, Best 1981). While on the nursery ground, calves do not appear to feed independently (Thomas & Taber 1984) and grow 2.8 cm d^{-1} on milk supplied by their fasting mothers (Best & Rüther 1992). Mothers leave the nursery ground and migrate to feeding grounds when their calves are 2-3 months old (Thomas & Taber 1984). Stable isotope and genetic analyses of skin biopsies of the PV right whales show that they feed over a broad isotopic range (implying a broad geographic range) and that calves inherit their foraging locations from their mothers (Valenzuela et al. 2009). The only definite connection between the Península Valdés whales and a feeding ground comes from four re-sightings of known individuals near South Georgia, the region of the western South Atlantic with the highest abundance of Antarctic Krill (*Euphausia superba*) (Atkinson et al. 2001; Best et al. 1993; Bonner 1987; Moore et al. 1999; Rowntree et al. 2001). Analyses of the first 30 years of aerial survey data have shown that females at PV have fewer calves than expected following years of low krill abundance off the island of South Georgia, which is believed to be a major feeding ground for all baleen whales in the western South Atlantic (Leaper et al. 2006).

In the following, we provide a summary of the unusual right whale mortality events at Península Valdés, Argentina from 2005-2009 and compare these recent events to the mortalities recorded since 1971. We examine the temporal and spatial distributions of strandings and between year differences in the lengths of dead calves (as an indicator of age). Given that no common cause of death has been found, diagnostic results from analysis of dead whales will be presented in future articles.

MATERIALS AND METHODS

Documentation of right whale deaths at Península Valdés

A record of dead whales found at Península Valdés has been maintained by the Whale Conservation Institute/Ocean Alliance's research team since 1971 and includes dead whales recorded during annual aerial surveys PV as well as incidental reports from local residents. Comparatively few dead whales were found in the first 20 years of the study. The population was much smaller in the early years, probably numbering only 500 whales in 1971. From 1994 through 2002 additional efforts were implemented to record dead whales through a reporting network, land-based surveys of beaches and the collection of measurements, tissue samples and baleen from dead whales to support studies comparing toxin loads of North and South Atlantic right whales (Angell et al. 2004), genetics (Rosenbaum et al. 2000) and foraging destinations (Rowntree et al. 2008). In 2003, a systematic survey effort (the Southern Right Whale Health Monitoring Program, SRWHMP) was initiated that covered the entire perimeter of Península Valdés with support from the US National Marine Fisheries Service. The SRWHMP has carried out the protocols described below since 2003, to document every whale that beaches at the Península. The SRWHMP is an ongoing collaborative project of several NGOs (Whale Conservation Institute/Ocean Alliance, Wildlife Conservation Society, Instituto de Conservación de Ballenas, Fundación Patagonia Natural, and Fundación Ecocentro).

Locating stranded whales. The SRWHMP field team is active during the six months that right whales are present at Península Valdés (mid-June to mid-December). The team locates whale carcasses through land surveys of the beaches where the whales concentrate, aerial surveys of the coast, and reports from members of a local stranding network. The network's 70-plus members include wildlife officers, fishermen, local inhabitants, whale-watch captains, dive-boat operators, tour-guides, boat captains, airplane pilots, researchers, non-governmental organizations and local authorities such as the Coast Guard. Due to a number of factors, the land-based and aerial survey effort has varied between seasons, though baseline levels of one or the other or a combination of both have always been sustained. Regardless, the stranding network consistently reported most of the dead whales (above 70%) recorded in the area from 2003-2009.

Necropsy protocol. Stranded animals are investigated following a right whale necropsy protocol developed for the program by M. Uhart, L. La Sala and L. Pozzi, based on materials by McLellan *et al.* (2004), F. Gulland (pers. comm.), A. Carribero (pers. comm.) and Geraci *et al.* (1993). When a stranded whale is reported, SRWHMP researchers travel as soon as possible to the stranding site. Once the whale is confirmed dead, the geographical location is recorded and photographs are taken. The state of decay of each carcass is coded, body measurements are taken and an external examination is carried out in search of scars, wounds and any other evidence of the cause of death or of human interaction. Depending on the state of decay, an internal examination or necropsy is also conducted (partially or completely) and a full set of diagnostic samples are collected. In all cases the animals' tails are tagged and notched to avoid recording repetitions.

RESULTS AND DISCUSSION

Description of the unusual mortality events (UME)

The 2005 UME. Forty-seven whales stranded at Península Valdés in 2005 with almost half of the deaths (22) occurring over a 26-day period from October 19 through November 14 (Fig. 3). Prior to 2003 the largest number of dead whales recorded in a year was 17 in 2000 (Fig. 2). The 2005 mortality event began on October 19 when three adult females washed onto adjacent beaches on the same day in Golfo San José (GSJ, the northern gulf of the Península, Fig. 1), followed by two more adult females in GSJ within the next two weeks. An unusual characteristic of the 2005 UME was the high proportion of adults and juveniles among the whales that died in the event in GSJ (6 adults, 4 juveniles and 2 calves). Fourteen calves died during the same period in Golfo Nuevo (GN, the southern gulf). More adults (7) died at PV in 2005 than has ever been recorded in a single year since the beginning of the study(Fig. 2).

The 2007 UME. Eighty-three right whales died at PV in 2007. Sixty-one deaths occurred between October 4 and December 15, with 58 whale carcasses beaching in GN and 3 in GSJ. One was an adult and 60 were calves. Dead animals appeared in bursts, the first in the first two weeks of October and the second in the beginning of November (Fig. 3).

The 2008 UME. Ninety-nine dead right whales beached off the Patagonian coast of Argentina in 2008. Ninety-six died at PV, and 3 adults stranded to the north of PV in Golfo San Matias. Again most of the mortality (67) at PV in 2008 occurred in GN. One-third of the whales died at the beginning of the nursery season in August and deaths continued at a steady rate with 3-12 deaths per week until October 22nd, by which time mortality totaled 82 whales over an 82-day period, including 76 calves. Mortalities occurred in two peaks in 2008, one beginning in mid-August and the other in the first week of October 1st (Fig. 3).

The 2009 UME. Seventy-nine whales died at PV in 2009. Most of the deaths occurred in GN (65), 13 were recorded in GSJ and one was found on the outer (oceanic) coast of PV. Most of the deaths occurred early in the season, with a peak (38 deaths including 37 calves) from mid August through mid September and a secondary peak (15 calves) from October 4-12 (Fig. 3).

Patterns in the number, timing, distribution and size of dead whales

Mortality rate through time. The number of dead whales recorded at PV increased annually from 1971 through 2002 at an overall rate very close to that estimated for the population as a whole (6.8% yr^{-1}, Cooke *et al*. 2003) (Fig. 4). Since 2005, however, the numbers have been much higher than expected based on the long-term historical trend, especially in the three recent years. Most right-whale females calve once every three years, and the three-year calving cohorts often differ in size. Thus consecutive years may differ in numbers of living and/or dead calves for purely demographic reasons. Trends caused by environmental changes may best be seen by examining averages over three-year periods. In 2007-2009, a mean of 79 calves died each year, compared to 21 per year during the previous three years (2004-2006) and 16 per year during 2001-2003. Thus the high-mortality years (2007-2009) show a 270% average increase in calf deaths over the 2004-2006 period, and a 385% increase over the 2001-2003 period. The increase in mortality for 2007-2009 is the highest recorded for any three-year period since the beginning of the PV right whale study in 1971, and it vastly exceeds the population's estimated growth rate from 1971-2000 (6.8% yr^{-1}, Cooke *et al.* 2003).

Changes in calf mortality through time can also be estimated by dividing the number of dead calves recorded in a year by the number of living calves recorded at the time of peak whale abundance during that year's aerial photographic survey. This ratio overestimates the absolute rate of calf mortality because living calves are sampled less fully than dead ones, but it scales each year's mortality to a direct measure of that year's calf production. The proportion of dead to living calves increases with time: 0.05 in 1971 – 1993, 0.09 in 1994 – 2002, 0.16 in 2003 – 2006, and 0.34 in 2007 – 2009.

Effort as a possible explanation for the recent increase in whale deaths. Some increase in mortality is expected from the increased effort implemented by the SRWHMP, beginning in 2003. But how large is this effect? How much of the post-2002 increase in recorded deaths is caused by increased probabilities that a given death will be detected, and how much of it is caused by genuinely increased rates of mortality? This is a difficult question because both the detection efficiency and the actual rates of mortality may have changed, and we have no way to directly estimate these factors independently of each other.

Here we will address a more restricted form of the question: Could increased effort account for *all* of the apparently increased mortality? For this purpose it will be conservative to assume that the first four years of the SRWHMP (2003-2006) saw typical (historic) rates of calf mortality, recognizing that this might be an insufficient timeframe to draw this type of conclusion. (We will focus on calves to control for potential heterogeneity in the causes of juvenile and adult mortality, and because calves are 90% of all dead whales). It can then be asked whether the seemingly very high calf mortalities of 2007-2009 fall significantly outside the range to be expected, given the detection efficiency implied by the data for 2003-2006, on the assumption that mortality rates in those years were in fact 'normal'. (If the apparently high mortality rates in 2003 and 2005 are part of a recent trend toward increased calf mortality, then this assumption will bias the analysis *against* the conclusion that the years 2007-2009 were truly extreme.)

Fig. 4 shows exponential fits to the raw data for the numbers of *living* calves counted during aerial surveys at the time of peak whale abundance (Fig. 4a), and *dead* calves counted on the beaches (Fig. 4b), for 1971-2002. Both fits give growth rates (6.8%/yr and 6.7%/yr respectively), very similar to the 6.8%/yr derived from Cooke's more sophisticated population model (Cooke et al. 2003). The similarity in rates suggests that *on average*, dead whales were detected in proportion to their actual numbers, although perhaps with low efficiency.

The improvement in efficiency initiated by the SRWHMP can then be estimated crudely by *elevating* the dead-calves curve so that it fits the data for the first four years of the SRWHMP (2003-2006, which for this purpose we are assuming to have 'normal' mortality rates) (Fig. 4b, upper curve). The curve is drawn in black during those four years, and in gray everywhere else, to indicate that its elevation reflects a fit to those four years only (while retaining the standard 6.7% increase in the number of dead calves from 1971-2002). This curve has an elevation roughly twice that of the lower curve (fit to the data for 1971-2002). Thus on the assumption that 2003-2006 in fact had historically 'normal' calf mortality rates, the SRWHMP would have roughly doubled the probability that a dead calf was detected.

This conclusion is probably conservative with respect to the hypothesis being tested, because it treats 2003 and 2005 as 'typical' years. If they are not, then we have overestimated the increase in efficiency of detection brought about by the SRWHMP. If we are overestimating the increase in efficiency, then we are underestimating the increase in mortality rates. However, even with an assumed doubling of the detection efficiency, the three most recent years (2007-2009) are clearly extraordinary.

More generally, on *any* assumption about the recent detection efficiency, mortality rates show great heterogeneity among years. On the assumption that the expected mortalities are those implied by the upper curve in Fig. 4b, the one- and two-tailed Poisson probabilities of seeing as many stranded calves as were actually seen in 2007-2009 are effectively zero (all less than 10^{-9}). Even in 2003-2006 (the years to which the curve is fit), mortality rates are significantly heterogeneous (higher than expected in 2003 and 2005, and lower than expected in 2004 and 2006).

Spatial distribution of mortalities (GSJ vs. GN). In addition to the 368 dead whales recorded by the SRWHMP at Valdés from 2003-2009, seven dead right whales were found on the Argentine coast outside of PV. In most years the number of living calves counted during annual aerial surveys at the time of peak whale abundance (end of September) has been slightly higher in GN than in GSJ. However, significantly more dead calves were found in GN than in GSJ ($X^2 = 44.4$, df = 1, $p = 3x10^{-11}$) (Fig. 5). GSJ is a protected marine reserve with little boat traffic (primarily scallop fishing boats), no towns and few human inhabitants. In contrast, GN is the site of Puerto Madryn (population 80,000), which is a center for commercial fishing and other industries (including a large aluminum plant) and has considerable large vessel traffic and whale-watching operations in Puerto Pirámide.

The higher proportion of dead calves in GN is a puzzling finding. From 1971 through 2000, dead whales were distributed almost equally between GSJ (50) and GN (41) with only 9 found along the eastern outer coast. The first year with higher mortality in GN than GSJ was in 1994. If the higher proportion of dead calves in GN relates to the microenvironment, the differential mortality could be caused by factors ranging from water temperature to harmful algal blooms to food availability late in the season. The whales have changed their distribution at PV over time.

In the 1980s, mothers abandoned the region along the outer coast where the highest proportion of mother/calf pairs concentrated and moved into GSJ and GN (Rowntree et al. 2001). It is possible that we are witnessing a proportional shift from GSJ into GN in the first decade of 2000.

Timing of peaks in mortality. In 2005 and 2007, most dead calves were found late in the nursery season (October through mid-November). In contrast, in 2008 and 2009, mortality peaked early in the season (mid-August through September) (Fig. 3). Secondary peaks occurred during the first two weeks of October in 2007, 2008 and 2009 (a time when sporadic feeding is first observed).

To assess the statistical significance of this temporal heterogeneity, each year was divided into four periods: *early* (June 1 – August 15, 76 days in all), *mid 1* (August 16 – 30 September, 45 days), *mid 2* (October 1 – 15 November, 45 days) and *late* (November 16 – December 31, 45 days). (The first period was summed over 76 days to make categories of comparable size, few living and dead whales are seen early in the nursery season.) Each calf stranding was assigned to the period in which it was first recorded. The resulting yearly distributions were then compared using conventional contingency chi-square analysis, which tests the null hypothesis that each year is a sample from the *same* underlying temporal distribution of calf mortalities.

The four years with the largest numbers of mortalities (2005, 2007, 2008, 2009) are highly significantly heterogeneous (mean = 71.7, 9 df, p = $7.1x10^{-12}$). This strong rejection of the null hypothesis is produced by the pattern mentioned above: a predominance of late mortalities in 2005 and 2007 *versus* a predominance of early mortalities in 2008 and 2009. Within each of these two pairs of years, there is no significant difference (mean = 5.51, 3 df, p = 0.14 for 2005 *versus* 2007; mean = 1.77, 3 df, p = 0.76 for 2008 *versus* 2009). However, between the two pairs of years, all four comparisons are highly significant (mean = 16.4, 3 df, p = $9.3x10^{-4}$ for 2005/2008; mean = 14.7, 3 df, p = 0.0021 for 2005/2009; mean = 48.7, 3 df, p = $1.5x10^{-10}$ for 2007/2008; mean = 40.9, 3 df, p = $7.3x10^{-9}$ for 2007/2009). The temporal distributions appear to be relatively uniform between August and October in the years with relatively low calf mortality (2003, 2004 and 2006) (Fig. 3), although the numbers are too small to support any strong conclusions about similarities or differences among these years or between them and the high-mortality years.

In summary, of the four years with unusually high levels of calf mortality, two (2005 and 2007) show a predominance of late mortality (October and early November) while the other two (2008 and 2009) show a predominance of early mortality (late August and September). This striking and highly significant difference suggests that somewhat different sets of causes may have increased rates of calf mortality in these two pairs of years.

Lengths of dead calves. Right whale calves grow rapidly in their first few months of life, making calf length a useful indicator of calf age. Best and Rüther (1992) used aerial photogrammetry to measure southern right whale mother-calf pairs on the nursery ground off South Africa, a population of similar size and with a similar timing of nursery season to that of the right whales at Península Valdés. They found a wide range of calf sizes (expressed as the distance from snout tip to fluke notch) at any one time. The median birth date for larger, multiparous mothers was mid-August with little year to year variation, while smaller, first-time mothers tended to give birth to smaller calves, on average later in the season but over a broader range of times (Best & Rüther 1992, Best 1994). The mean length at birth for southern right whales is estimated to be 5.5 - 6.1 m (Whitehead & Payne 1981, Best 1981). Calves measured more than once in a season grew at an average rate of 2.8 cm d^{-1} (SD 0.7), with calves of all sizes growing at similar rates (Best and Rüther 1992). Living calves ranged in length from 4.53 to 9.24 m throughout the nursery season.

The lengths of 293 calf carcasses measured at Península Valdés from 2003 through 2009 ranged from 2.18 to 9.83 m and showed a considerable range in size at any given time in the season (Figs. 6 & 7). Small dead calves (5 m or less) were found from June through October with the majority in each year being found after August 31 (Fig. 6), indicating that calves are born throughout the nursery season.

The lengths of dead calves in 2005 and 2007 increased as the season progressed (at rates of 2.9 and 2.4 cm d^{-1}, respectively), but in 2008 and 2009 the lengths of dead calves showed no significant trend over the season (Figs. 6 & 7). An analysis of covariance (ANCOVA) established the statistical significance of this apparent difference between the trends in these two sets of years with different patterns of mortality ($t = 5.9$, $p <0.0001$). In addition, the range and standard deviation of the lengths of dead calves in 2005 and 2007 was broader (3.87 to 9.86 m, SD = 1.46) than in 2008 and 2009 (3.4 to 7.76 m, SD = 0.85) when no large dead calves were found. These overall length differences are not unexpected, because calves that die early in the season (as in 2008 and 2009) probably die shortly after birth and are expected to be smaller than those that die later in the season (as in 2005 and 2007).

Some unanticipated trends appear, however, when the seasonal changes in lengths of dead calves are compared for years with high mortalities early and late in the nursery season. In both kinds of years, the mean lengths of dead calves in the first time period (June 1 - August 15) are similar, but the mean lengths begin to diverge in the following period. In the second period (August 16 -- September 30), mean calf lengths are greater in 2008 and 2009 than in 2005 and 2007 (Fig. 6). In the last two periods (October 1 - December 31) this difference *reverses*, with dead calves being larger in 2005 and 2007 than in 2008 and 2009.

The interaction between years and time periods is highly significant in a two-way ANOVA of calf length, as is the main effect of time period, while the main effect of year is marginally significant ($p = 0.04$, see Table 2). When 2005 and 2007 are analyzed separately, there is no effect of years (nor any interaction between years and time periods), although the main effect of time periods remains highly significant. A qualitatively identical result is obtained when 2008 and 2009 are analyzed separately (Table 2). These findings are consistent with the hypothesis that the excess calf mortalities had somewhat different causes in these two sets of years. When the data are combined for 2005+2007 (late mortality) and for 2008+2009 (early mortality), and a two-way ANOVA is carried out on these two sets of years, both of the main effects (and their interaction) are highly significant (Table 2).

In summary, calves dying early in the season tend to be small (and presumably very young) in all four years, and there are at least a few late young calf mortalities in all four years as well. The difference is that highly unusual numbers of larger (hence older) calves died late in the seasons of 2005 and 2007, and that highly unusual numbers of small calves died early in the seasons of 2008 and 2009.

The only time when dead calves were larger in 2008+2009 than in 2005+2007 was during the *mid 1* period (August 16 - September 30)($F = 22.3$, df = 1, $p < 0.0001$)(Fig. 7). This difference could be explained if many of the calves dying then had been born to more experienced, multiparous mothers, which tend to have larger calves (Best and Rüther 1992).The size distribution of dead calves at Península Valdés from June through August in 2008+2009 is very similar to that of living calves measured by Best and Rüther (1992) during the same months off South Africa (ranges 4.10 - 7.04 m and 4.53 - 7.38 m, respectively), suggesting that the distribution of dead calf lengths in these years is close to the typical distribution for living calves. By contrast, the range of dead calf lengths during these months in 2005 and 2007 is much narrower (4.05 – 4.48 m), suggesting that they could have been mainly smaller calves of younger, less experienced mothers. Thus the relative abundance of larger calves in the early-season mortalities of 2008 and 2009 (Figs. 6 & 7) could indicate that calves of older as well as younger mothers died in those years, from some population-wide effect such as nutritional stress or the lingering effects of a widespread environmental disturbance on the feeding grounds that reduced the viabilities of calves regardless of their mothers' experience and size.

On this interpretation, the later mortalities of larger (older) calves in 2005 and 2007 may have been caused by a more local and immediate factor that took effect only shortly before the mortalities. This is suggested by the apparently normal growth of many calves before death. The calves that died after September 30 in 2005 and 2007 were 7.3 m long on average, which is 1.2 m longer than the average mean length at birth (6.1 m) estimated by Best (1994). The lengths of dead calves in 2005+2007 increased with day of death at 2.6 cm d^{-1} (Fig. 6), a rate remarkably close to the actual growth rate of 2.8 cm/d estimated by Best & Rüther (1992) for living calves. Thus, it can be inferred that these larger calves had grown for some time, at apparently normal rates, indicating that they and their mothers were probably healthy before the calves died. One possible cause for the sudden death of apparently healthy right whales is harmful algal blooms (HABs), which are known to occur at PV and have affected baleen whales (Geraci *et al.* 1989). The mean lengths of calves dying in the last two periods of 2005 and 2007 (*mid 2* and *late*) are not significantly different, probably because many of the mothers of older (larger) calves would have left PV for the feeding grounds by late October and November (Best & Rüther 1992, Thomas & Taber 1984).

The early high mortalities in 2008 and 2009 could have been caused by biotoxins that pregnant females ingested on their feeding grounds as has been observed in California sea lions (Brodie et al. 2006, Ramsdell & Zabka 2008), but alternatively these mortalities could have been caused by *failures* to ingest adequate quantities or qualities of prey on those same feeding grounds. During the *mid 1* period, dead calves were actually larger in 2008 and 2009 than in 2005 and 2007, consistent with the hypothesis that older, larger, multiparous females were experiencing elevated rates of calf mortality in much the same way as younger, smaller, primiparous females. On this hypothesis, the cause is most plausibly some kind of population-wide effect that is experienced by all females regardless of age, size and experience. Between 1971 and 2000, the PV whales had fewer calves than expected following years of low krill abundance at South Georgia (Leaper *et al.* 2006). Other krill predators that forage and breed at South Georgia (*e.g.,* fur seals and Gentoo penguins) also showed elevated rates of reproductive failure in those years (Trathan et al. 2006).

CONCLUSION

The PV right whale population grew at an average rate of 6.8% per year from 1971 through 2000 when it was estimated to include 697 adult females and 213 calves (Cooke et al. 2003). The growth rate has not been re-estimated from aerial photographic survey data since the die-offs began, but if the population had continued to grow at roughly the same rate, then it would have produced an estimated 361 calves in 2008. In 2007-2009, we detected an average of 79 dead calves per year, which is more than a fifth of the calves estimated to have been born in 2008 (79/361 = 0.22). This would appear to be a conservative estimate of the recent calf mortality rate, for two reasons. First, the recent population growth rate may be less than 6.8%, owing in part to the increased rate of calf mortality; if so, then the number of calves born in 2008 would be less than 361. Second, we undoubtedly fail to detect some calves that die; if so, the recent average number of mortalities is probably greater than 79. A 20% calf mortality rate seems alarmingly high, but these facts suggest that the actual recent rate may be even higher.

The timing of the unusual mortalities of right whales at PV differed between years with significantly more deaths occurring early in the nursery season in 2008 and 2009 and late in the season in 2005 and 2007. Calves that died late in the season in 2005 and 2007 were much larger than newborns, indicating that they had grown at normal rates before dying. Their growth implies that they were probably healthy before death and succumbed to some sudden cause of death in 2005 and 2007. In 2008 and 2009, nutritional stress could have reduced the blubber reserves of pregnant females causing calves to die shortly after birth. While many samples and much information has been gathered to date, common significant lesions or pathologic processes (e.g. infectious disease) to explain the yearly or recurrent mortalities have not been identified. Therefore, additional data is needed to determine the causes for the recent deaths. Ongoing monitoring for independent, multifactorial/interrelated or concurrent disease processes, including infectious, toxic or nutritional disease, genetic or environmental factors including food availability and maternal and calf fitness are critical for establishing the cause(s) of the recent recurrent, significant mortality of young right whales at Península Valdés.

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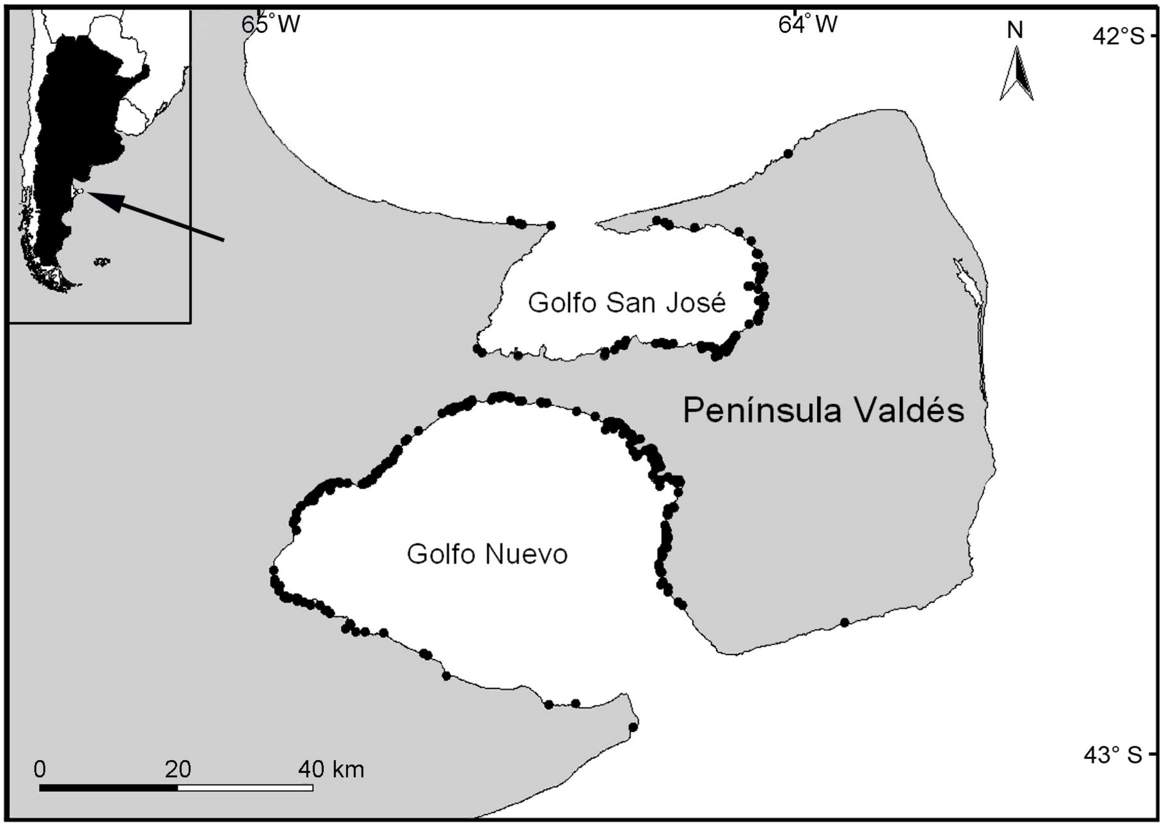

Fig. 1. *Eubalaena australis.* Map of Peninsula Valdes, Argentina showing the distribution of right whales strandings (black circles) from 2003 through 2009.

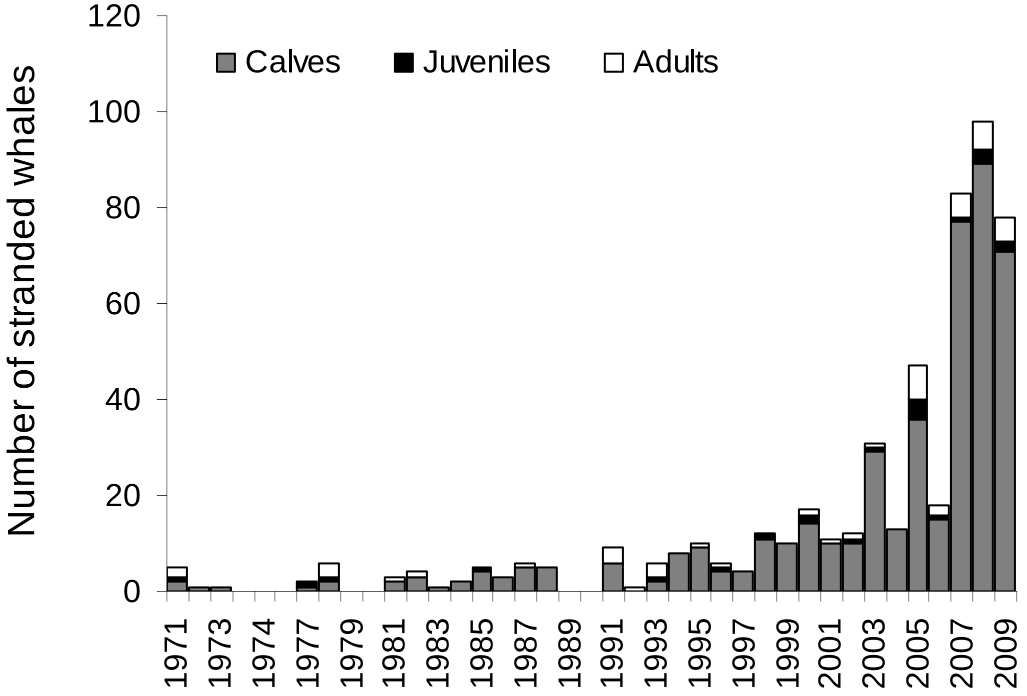

Fig. 2. *Eubalaena australis*. Distribution of age classes among right whales that died at Peninsula Valdes from 1971 through 2009.

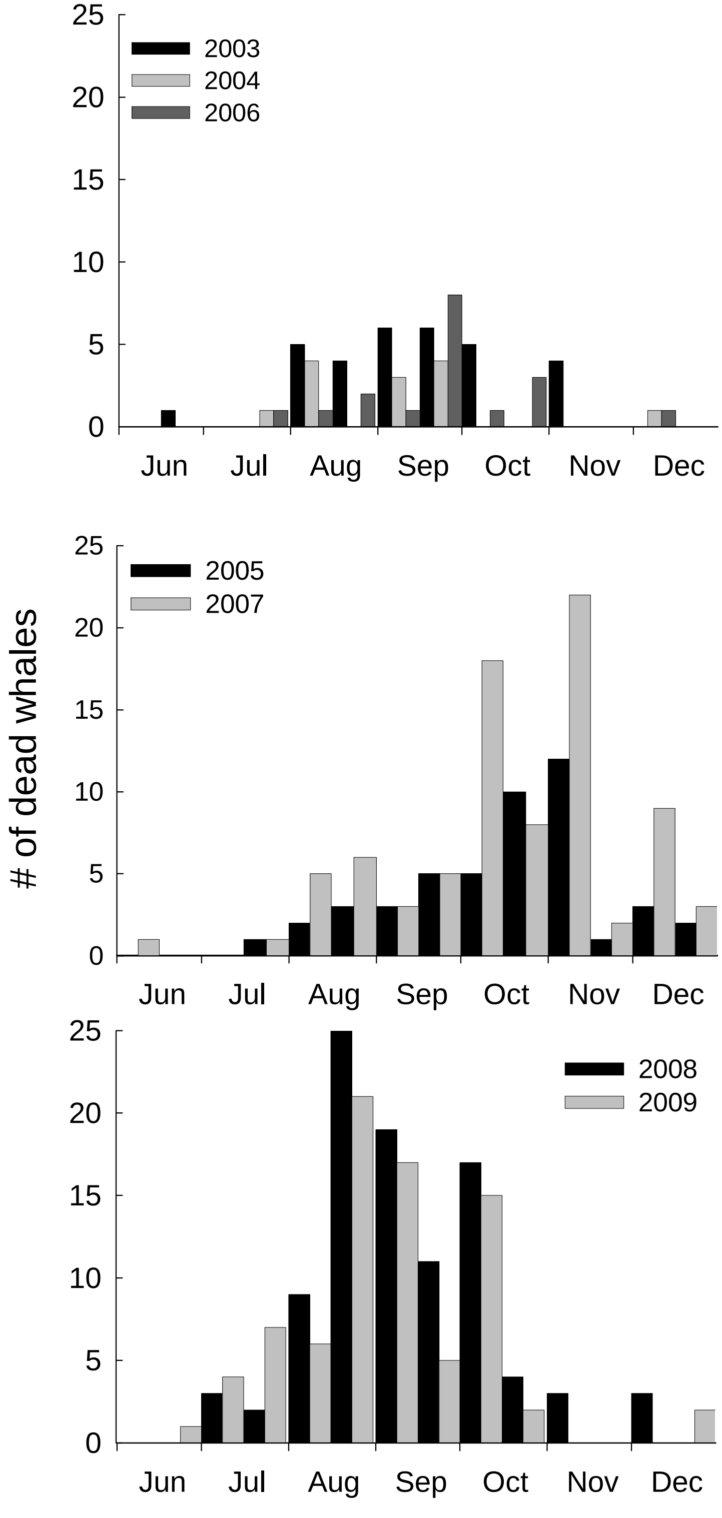

Fig. 3. *Eubalaena australis*. Biweekly distribution of right whale deaths during the nursery season at Peninsula Valdes from 2003 through 2009. The graphs are grouped into years with low mortalities (2003, 2004, 2006) and years when peaks in mortality occurred late (2005 and 2007) or early (2008 and 2009) in the season.

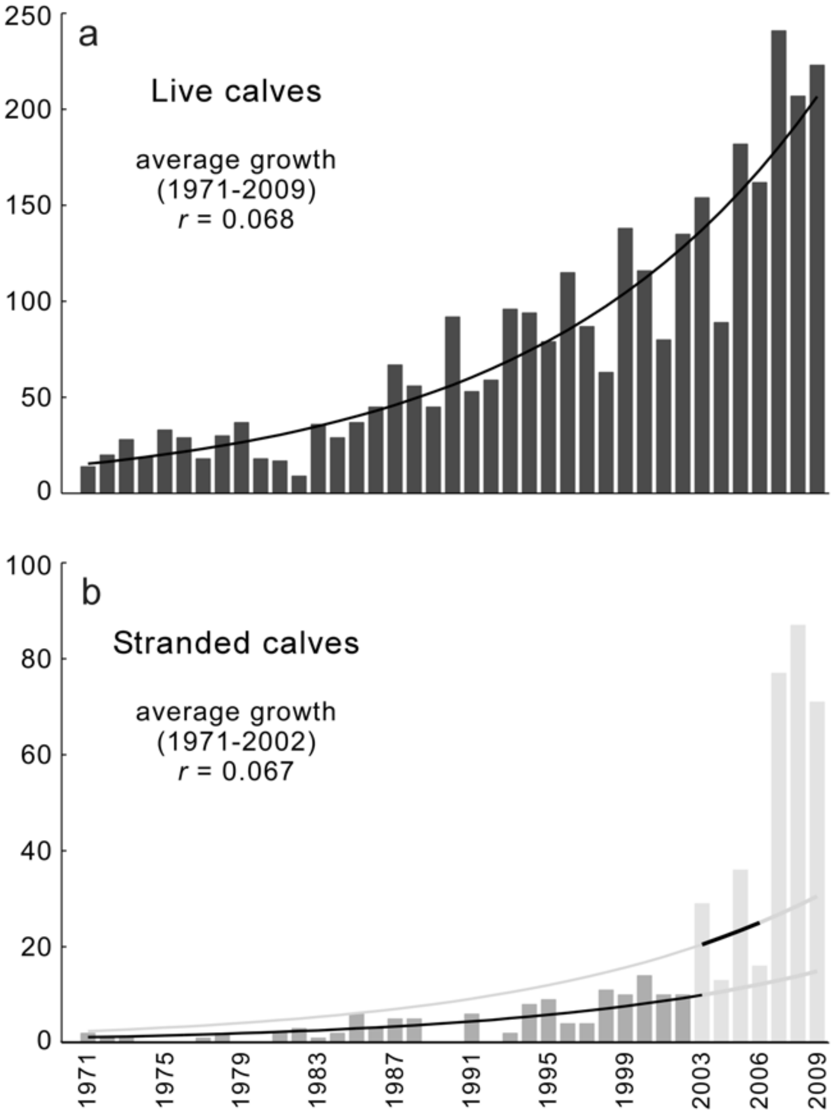

Fig 4. *Eubalaena australis.* a) Numbers of living calves counted during aerial photographic surveys at time of peak whale abundance from 1971-2009 (above) and b) numbers of dead calves found on the shores of Peninsula Valdes from 1971-2009 (below). Curves are fits of the standard exponential population growth function to the raw data. In the lower panel (dead calves), the darker lines indicate the years of data used to fit each curve, 1971-2002 for the lower curve (prior to the SRWHMP) and 2003-2006 for the upper curve (when the SRWHMP was in operation).

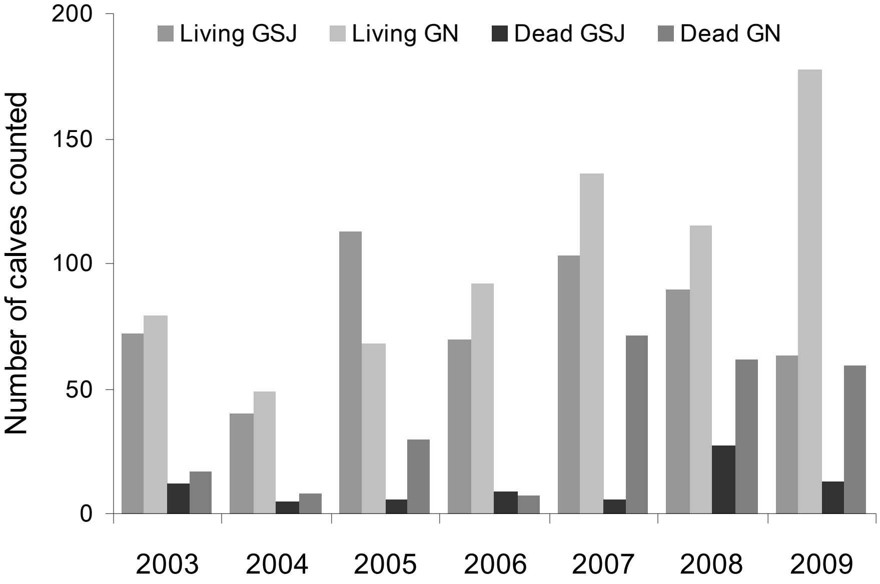

Fig. 5. *Eubalaena australis.* The number of living (lighter greys) versus dead right whale calves (black and darker grey) counted between the two gulfs of Peninsula Valdes, Golfo San Jose (GSJ) and Golfo Nuevo (GN), from 2003 through 2009. Living calves were distributed almost equally between the two gulfs at the time of peak whale abundance but more dead calves were found Golfo Nuevo in high mortality years.

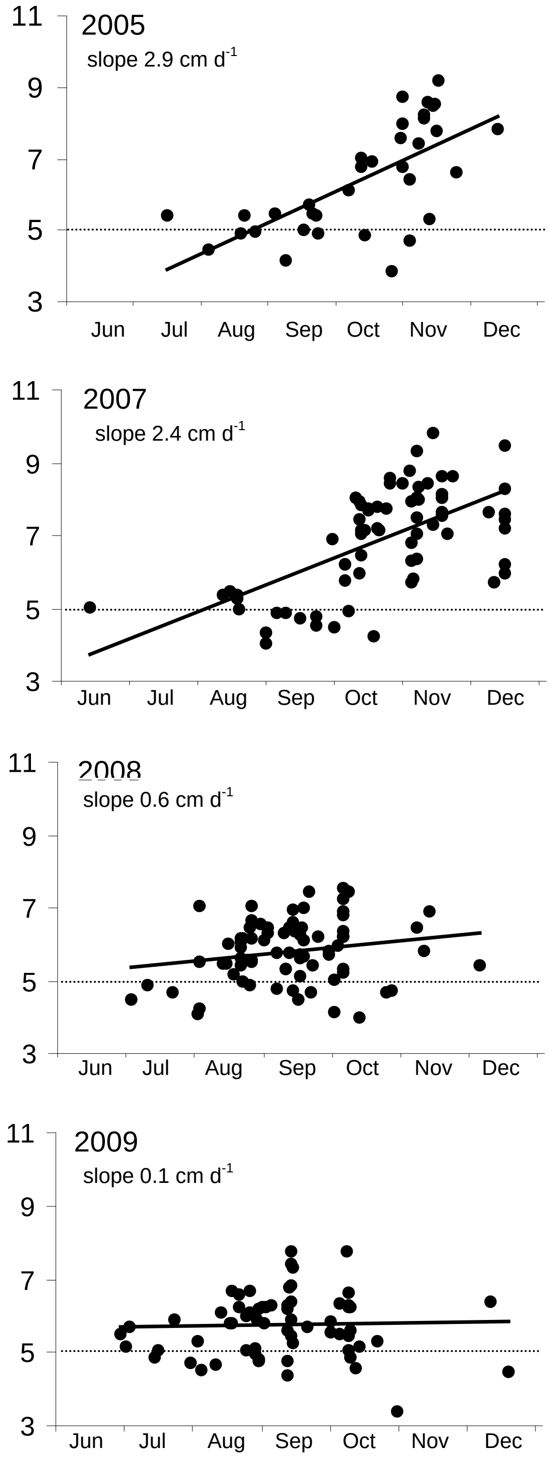

Fig. 6. *Eubalaena australis*. Lengths of dead calves on the day they were found in years with high calf mortalities. The increase in calf lengths throughout the season is shown in each graph beneath the year label. Lengths are straight-line measurements from snout-tip to fluke notch. Dead calves below 5 m dotted line are considered to be very small.

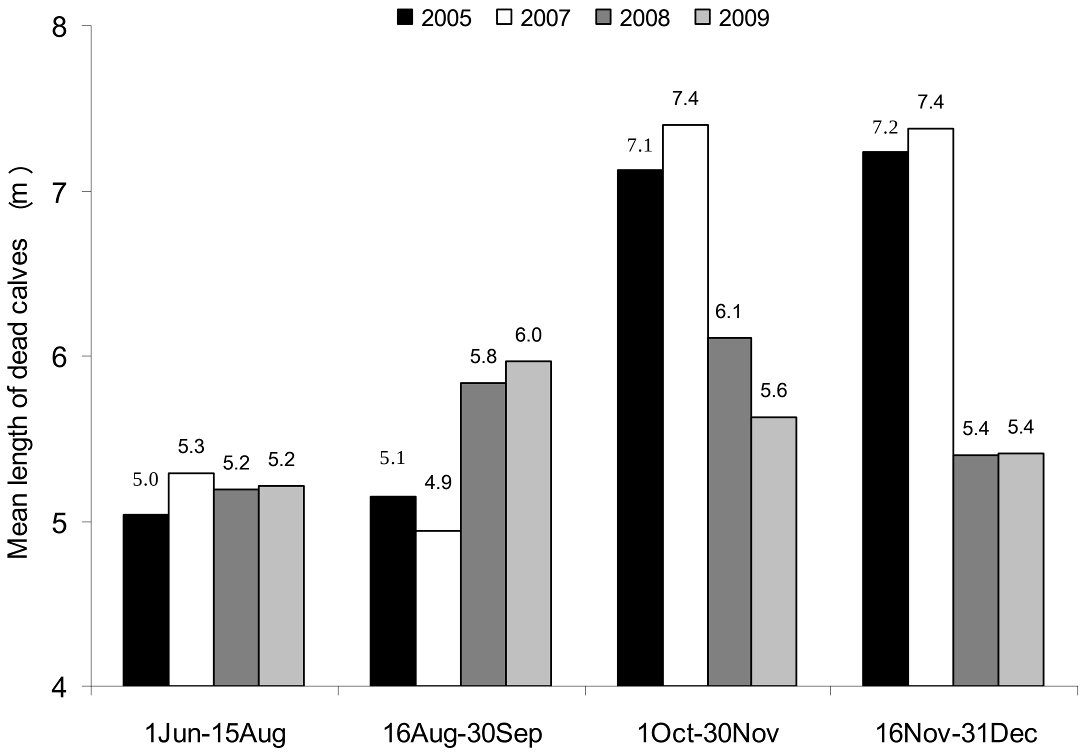

Fig. 7. *Eubalaena australis*. The mean lengths of dead calves divided into the time periods in which they died. The graph includes only the years with high mortalities (2005, 2007, 2008, 2009).

Table 1. *Eubalaena australis.* The number and age categories of dead whales recorded at Península Valdés since 2003. Ninety percent of the dead whales were calves.

	2003	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**Total**	**% of Total**
Calves	29	13	36	16	77	89	72	332	90%
Juveniles	1	0	4	1	1	0	1	8	2%
Adults	1	0	7	1	5	4	5	23	6%
Unknown	0	0	0	0	0	3	2	5	1%
Total	31	13	47	18	83	96	80	368	100%

Table 2. *Eubalaena australis.* Results of analysis of variance (ANOVA) to explore the relationship between year, time period and year + time period on the lengths of dead calves.

Factors	*n*	df	*F*	*p*	Significance
All years separately	230	15	11.5	<0.0001	***
yr		3	2.8	0.0424	*
period		3	19.2	<0.0001	***
yr x period		9	6.3	<0.0001	***
2005&2007 only	98	7	10.5	<0.0001	***
yr		1	0.1	0.7103	
period		3	22.9	<0.0001	***
yr x period		3	0.2	0.9263	
2008&2009 only	132	7	2.3	0.0312	*
yr		1	0.1	0.7784	
period		3	4.2	0.0068	**
yr x period		3	1.1	0.3641	
Early & late years (05&07;08&09)	230	7	24.6	<0.0001	***
early & late		1	8.4	0.0041	**
period		3	21.3	<0.0001	***
early&late x period		3	19.0	<0.0001	***