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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 two-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 two-year intervals are expected to increase when perinatal (late-term fetus and neonatal calf) mortality increases. Four- and five- 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 22% 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). But then the numbers of dead calves increased sharply, totaling 593 in nine of the 11 years between 2003 and 2013 (Fig. 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).

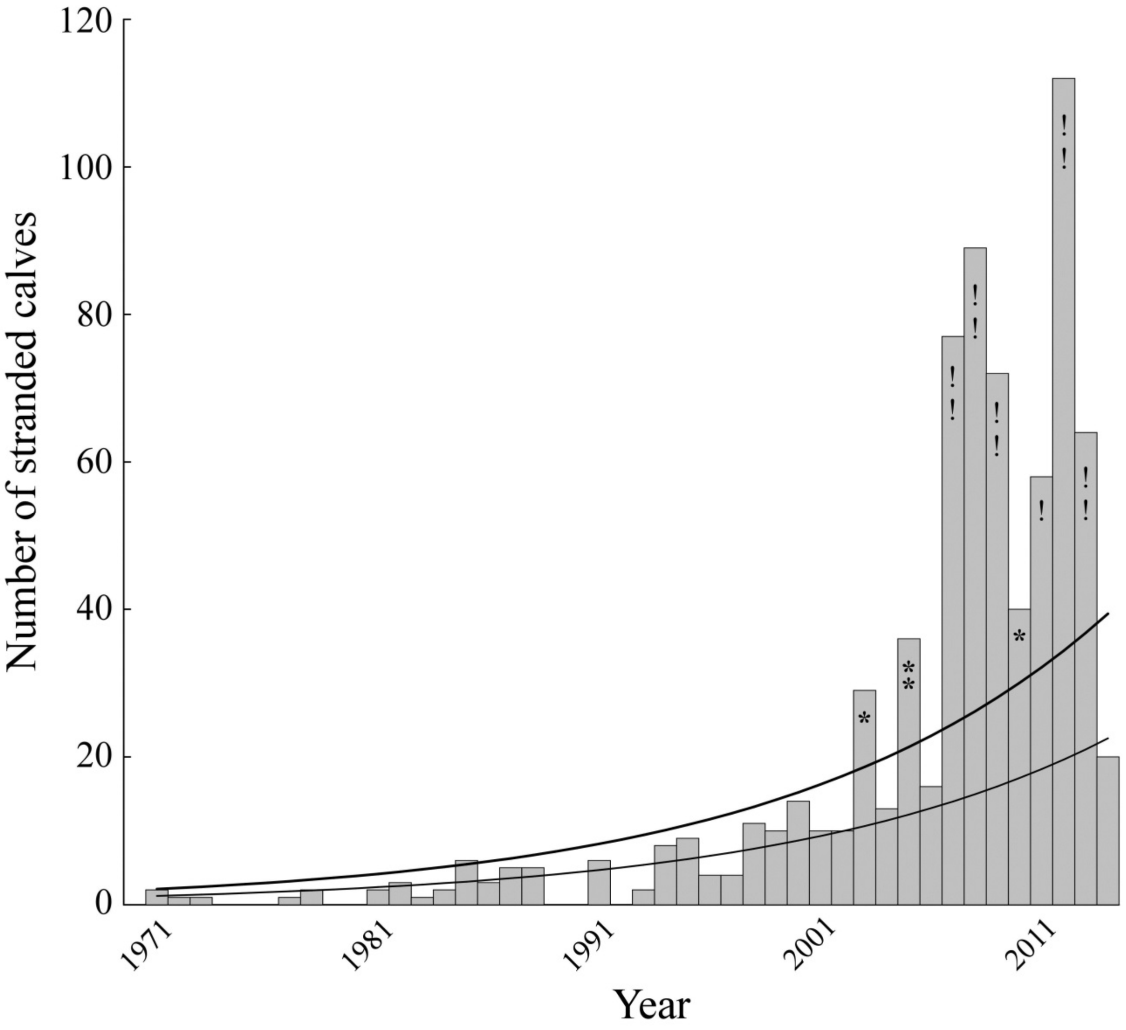

Fig. 1. Numbers of stranded calves recorded at Península Valdés, 1971-2013. The lower curve (thinner line) is an exponential fit to the data for 1971-2002, assuming a 6.8% yearly rate of increase. The upper curve (heavier line) shows the numbers that would be expected, on average, if the detection efficiency 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).

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 three-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. 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. 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. 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. 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. 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. But even if most two-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 two-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.

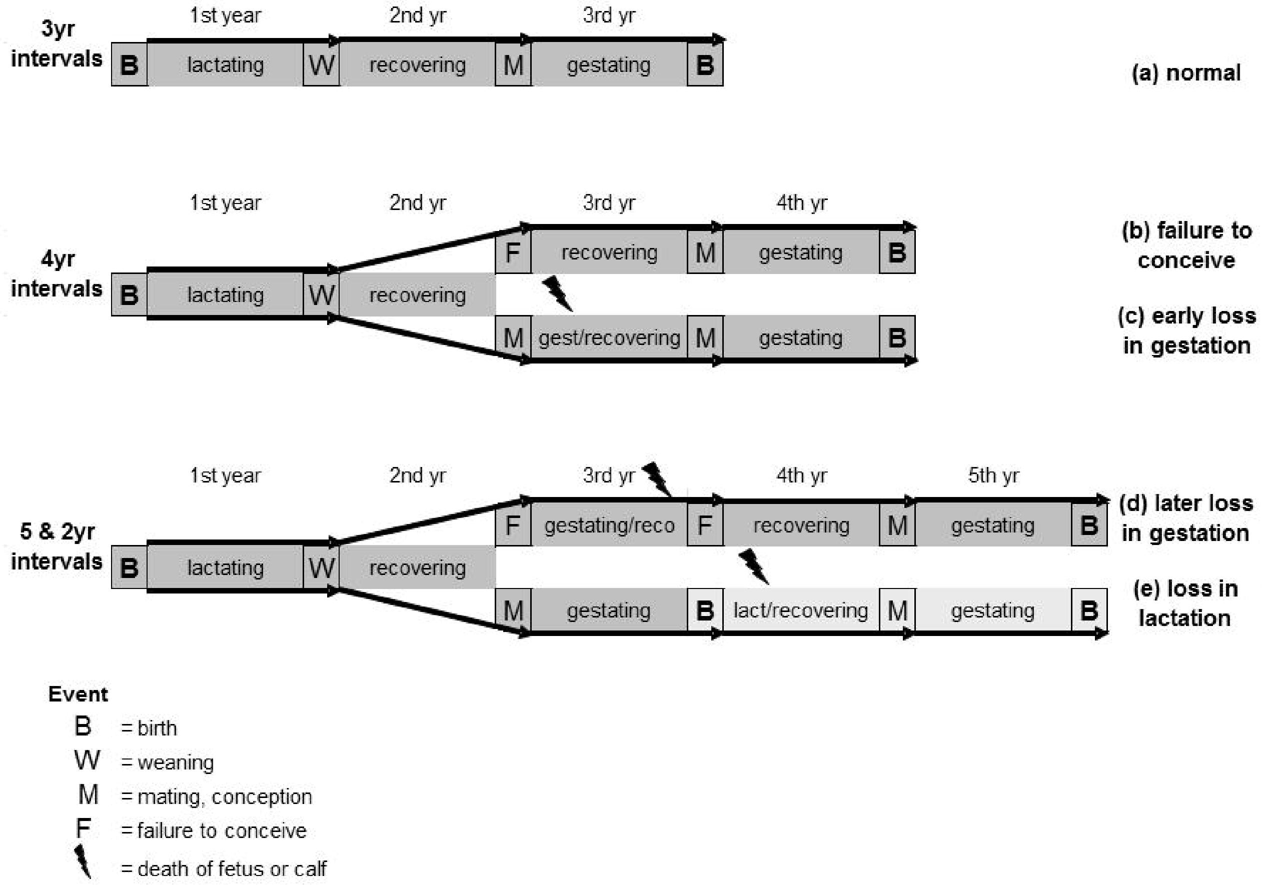

Fig. 2. Five potential scenarios for explaining normal (3-year) and abnormal (2-, 4- and 5-year) calving intervals in right whale species. The lightning bolt symbol indicates fetus or calf loss. Years are indicated on top of each scenario. (a) 3-year calving interval or normal. (b) 4-year interval with 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), mating (M), weaning (W), failure to conceive (F).

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 two-year intervals beginning then are completed in 2011, 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 number of dead calves and 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. (2003) provide such estimates for 1971-2000; we smoothed those numbers and extrapolated to include 2001-09 by fitting an exponential growth model (Appendix 1).

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. 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. 1 and Appendix 2).

Comparison of reproductive failures and successes with female age,
survey year, relative number of dead calves and
high- versus 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- or 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, surveyed 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 1). 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.

Table 1. Estimated parameters used in our 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 second year) that survive to enter the resting cohort at age 8	0.92	Cooke et al. 2001
Equilibrium annual growth	0.065	This article

The four alternative scenarios all share the same set of fixed parameters for the first 34 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 20 years), owing to the stresses induced by increased pregnancy and parturition rates. And 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 394 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 13% in the 2000s (a five-fold 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 34% of intervals were not 3-year) than in normal low-mortality years (20% not 3-year) (p = 0.007). Table 2 shows the numbers of 2-, 3-, 4- and 5-year intervals separately for both kinds of years, and Figure 3 shows the numbers of 2- and 3-

year intervals separately for all years except 2009. Two-year intervals began vastly more often in high-mortality years (21.7% of the high-mortality total) than in low-mortality years (3% of the low-mortality total) ($p = 2\text{x}10^{-13}$), but 4- and 5-year intervals showed no significant or notable differences.

Table 2. Observed calving intervals (“successful”: 3-years, “failures”: 2-, 4- and 5-years) of the southern right whales at Península Valdés, Argentina for the period 1971-2009.

Calving interval	*Lower-mortality years*[a]		*Higher-mortality years*[b]	
2-year	20	3.0%	18	21.7%
3-year	538	79.9%	55	66.3%
4-year	46	6.8%	5	6.0%
5-year	69	10.3%	5	6.0%
Total	673	100%	83	100%

[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. 2).*

[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. 2).*

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.

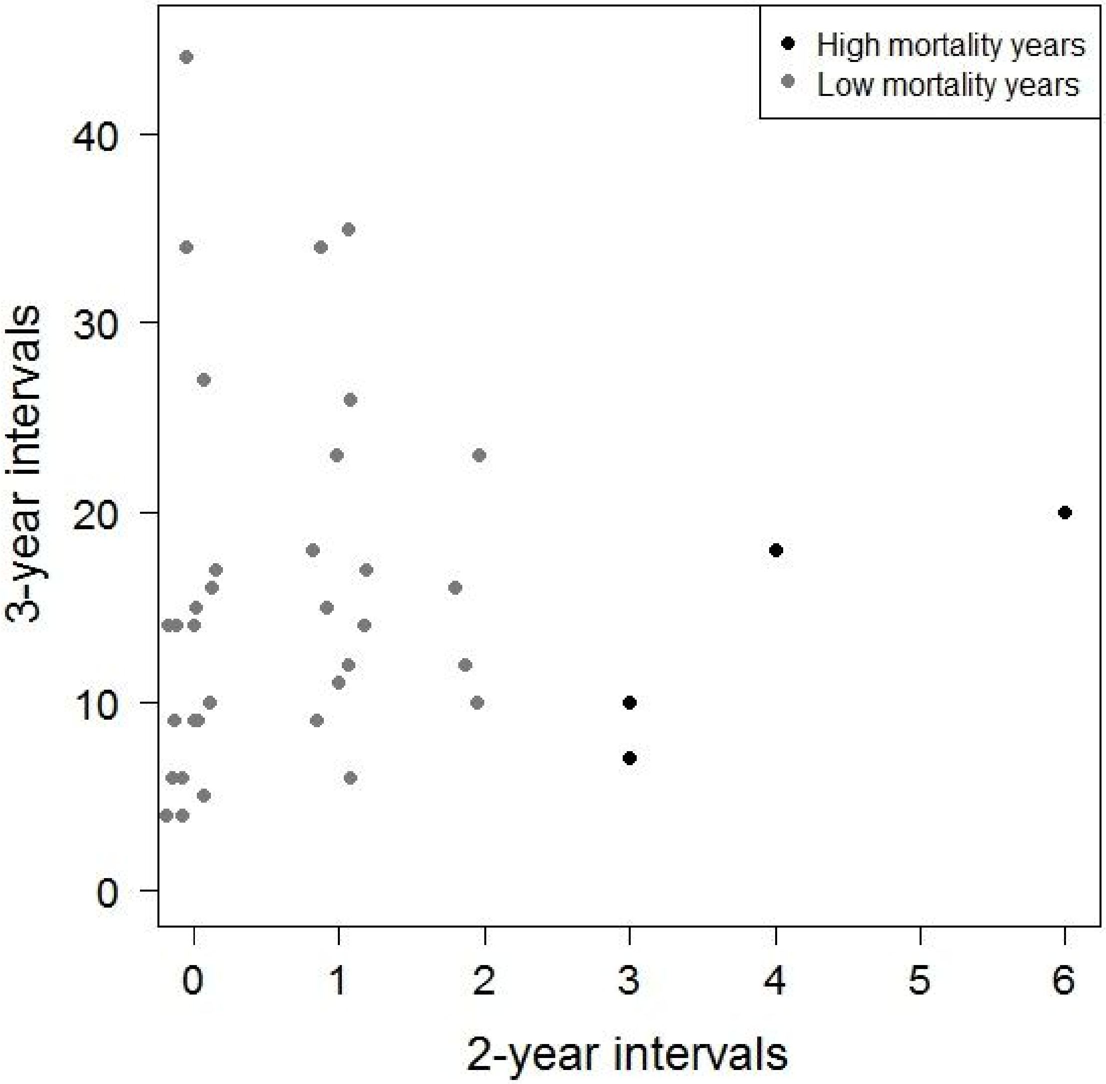

Fig. 3. Number of 3-year and 2-year calving interval cases per year (1971-2008). Black filled dots indicate low-mortality years (1971-2002, 2004 and 2006) and empty rhombi indicate high-mortality years (2003, 2005 and 2007-08). 2009 is not shown.

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- or 5-year intervals) did not depend on a mother's estimated age ($p = 0.5$) 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: $X^2 = 0.08$, $p = 0.78$; 4-year intervals: $X^2 = 0.08$, $p = 0.77$; 5-year-intervals: $X^2 = 0.49$, $p = 0.78$) (Table 3).

Table 3. Observed calving intervals in inexperienced and experienced southern right whale females at Península Valdés, Argentina for the period 1971-2009.

Calving interval	*Inexperienced females*[a]	*Experienced females*[b]
2-year	30	8
3-year	448	145
4-year	40	11
5-year	54	20
Total	572	184

[a] *"Inexperienced females" are females with up to three calves observed.*
[b] *"Experienced females" years are females with more than three calves observed.*

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 not correlated with the relative numbers of dead calves on the beaches ($p = 0.1$), nor were the proportions of 4- and 5-year intervals separately ($p = 0.62$ and $p = 0.08$, respectively). However, 2-year intervals considered separately were very highly significantly correlated with the relative numbers of dead calves ($p = 1.62\text{x}10^{-08}$).

Age at first parturition does not change over decades

The mean age at first recorded parturition was 11.6 ± 4.8 years with a range of 6 to 33 years. The decadal means did not differ significantly ($p = 0.3$).

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. 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 Figure 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. And 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. 4).

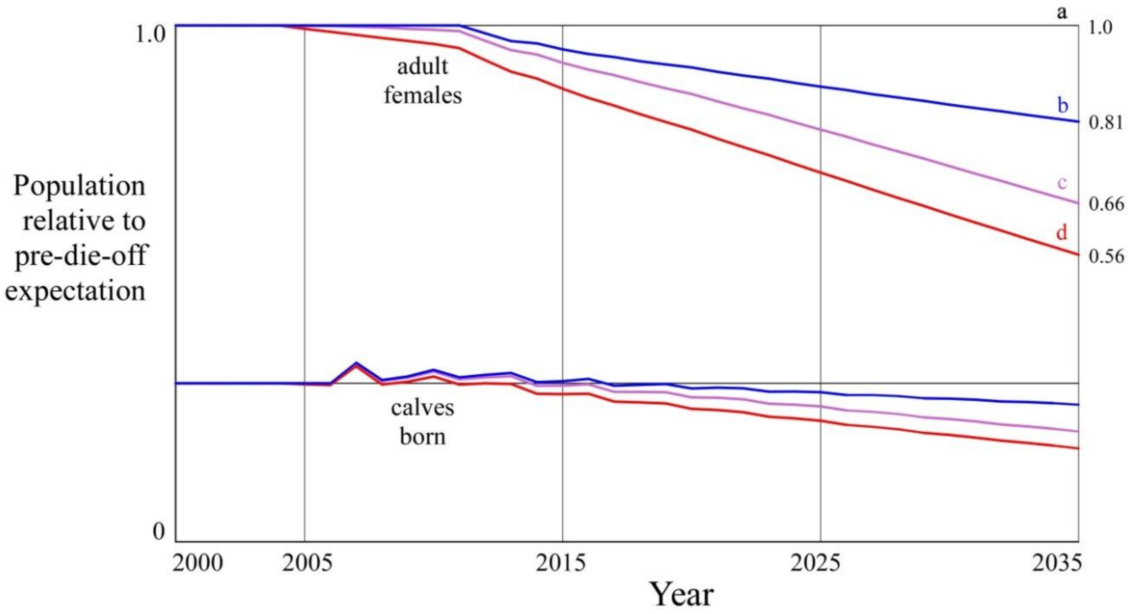

Fig. 4. Relative female population sizes by year under four scenarios. Trajectories are shown separately for adult females and calves, normalized by the population size expected under the null scenario that no higher-mortality years occur (scenario 'a', horizontal black lines). Under scenario 'b' (blue 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 higher 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 two-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.

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 (21.7% of all intervals, see Table 2) than in typical low-mortality years (3.0%). Taken at face value, this difference would imply that the calf mortality rate was 21.7/3.0 = 7.2 times higher in those five high-mortality years than in typical years, on average, which is a larger difference than suggested by Figure 1 and Appendix 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 failure to *complete* a pregnancy. But if apparent 5-year intervals often result from unrecorded 2-year intervals, 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 result from food limitation rather than from calf loss triggered by other kinds of environmental insults. 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. 2d, Appendix 3). 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 12.7%, while the lower limit on the proportion during low-mortality years is 8.1% (or

6.9% 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, two-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 & 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 10 or 11 years in 1910-1920, but later in the 20th century they often reached sexual maturity at 6 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. And 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) 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 1999-2013. 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. 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. 4*a*) 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. 4*b*, 4*c*, 4*d*). 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 higher-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 higher-mortality years survive to enter the reproductive population. In addition, fewer calves are produced because fewer mothers are recruited from higher-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 (unsuccessfully) calving at shorter intervals.

In summary, juvenile females 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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Appendix 1

Smoothed and extrapolated fit to the calving estimates in Cooke et al.(2003)

Assume r = 0.068. Estimated n0(1970) = 26.4.
"Average" is the cumulative mean difference between the estimated calf production (est) and the smoothed fit.

year	**est**	**smooth**	**diff**	**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	0.10
1982	55	59.7	-4.7	-0.30
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	0.70
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	135.0	-2.0	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	203.0	9.0	0.47
2001		217.3		
2002		232.6		
2003		249.0		
2004		266.5		
2005		285.2		
2006		305.3		
2007		326.8		
2008		349.8		
2009		374.4		

Appendix 2

Assume population growth rate of 0.068.
Fit predicted calf strandings to those observed in 1971-2002.
Intercept minimizing SS for raw(n) = 1.13
Assume SRWHMP increases detection efficiency by 75%
"<" indicates significantly ***too few*** strandings, ">" = ***too many***.

```
year   obs    pred(71-02)    pred*175%    P(obs|175%)

1971     2    1.2 ( -0.8)    2.1 (  0.1)  0.64513816
1972     1    1.3 (  0.3)    2.3 (  1.3)  0.33886729
1973     1    1.4 (  0.4)    2.4 (  1.4)  0.30303657
1974     0    1.5 (  1.5)    2.6 (  2.6)  0.07459806
1975     0    1.6 (  1.6)    2.8 (  2.8)  0.06214507
1976     0    1.7 (  1.7)    3.0 (  3.0)  0.05110982
1977     1    1.8 (  0.8)    3.2 (  2.2)  0.17342782
1978     2    1.9 ( -0.1)    3.4 (  1.4)  0.33839071
1979     0    2.1 (  2.1)    3.6 (  3.6)  0.02607602 <
1980     0    2.2 (  2.2)    3.9 (  3.9)  0.02017435 <
1981     2    2.4 (  0.4)    4.2 (  2.2)  0.21316411
1982     3    2.6 ( -0.4)    4.5 (  1.5)  0.34704384
1983     1    2.7 (  1.7)    4.8 (  3.8)  0.04826219 <
1984     2    2.9 (  0.9)    5.1 (  3.1)  0.11463008
1985     6    3.1 ( -2.9)    5.5 ( -0.5)  0.46831745
1986     3    3.4 (  0.4)    5.9 (  2.9)  0.16319872
1987     5    3.6 ( -1.4)    6.3 (  1.3)  0.40137156
1988     5    3.8 ( -1.2)    6.7 (  1.7)  0.33719680
1989     0    4.1 (  4.1)    7.2 (  7.2)  0.00074792 <
1990     0    4.4 (  4.4)    7.7 (  7.7)  0.00045069 <
1991     6    4.7 ( -1.3)    8.2 (  2.2)  0.28416090
1992     0    5.0 (  5.0)    8.8 (  8.8)  0.00014669 <
1993     2    5.4 (  3.4)    9.4 (  7.4)  0.00434192 <
1994     8    5.8 ( -2.2)   10.1 (  2.1)  0.32022779
1995     9    6.2 ( -2.8)   10.8 (  1.8)  0.35983065
1996     4    6.6 (  2.6)   11.6 (  7.6)  0.01012629 <
1997     4    7.1 (  3.1)   12.4 (  8.4)  0.00573088 <
1998    11    7.6 ( -3.4)   13.3 (  2.3)  0.32592278
1999    10    8.1 ( -1.9)   14.2 (  4.2)  0.16227537
2000    14    8.7 ( -5.3)   15.2 (  1.2)  0.44448133
2001    10    9.3 ( -0.7)   16.3 (  6.3)  0.06838907
2002    10   10.0 ( -0.0)   17.4 (  7.4)  0.04019009 <
2003    29   10.7 (-18.3)   18.6 (-10.4)  0.01575488  >
2004    13   11.4 ( -1.6)   20.0 (  7.0)  0.06716282
2005    36   12.2 (-23.8)   21.4 (-14.6)  0.00238393  >
2006    16   13.1 ( -2.9)   22.9 (  6.9)  0.08605788
2007    77   14.0 (-63.0)   24.5 (-52.5)  0.00000000  >
2008    89   15.0 (-74.0)   26.2 (-62.8)  0.00000000  >
2009    72   16.0 (-56.0)   28.0 (-44.0)  0.00000000  >
2010    40   17.2 (-22.8)   30.0 (-10.0)  0.04660509  >
2011    58   18.4 (-39.6)   32.1 (-25.9)  0.00002562  >
2012   112   19.7 (-92.3)   34.4 (-77.6)  0.00000000  >
2013    64   21.0 (-43.0)   36.8 (-27.2)  0.00003060  >
```

Appendix 3

Directly observed calving intervals beginning in 1971-2009

High-mortality years are marked "high" in the last column.

	calving interval				calf mort year
	2	3	4	5	
1971		4	1		
1972		16	3		
1973	1	18	4	1	
1974		4	1	2	
1975		10	1	1	
1976		14	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	26	2	3	
1985		17		1	
1986	2	16	2		
1987		44	1	2	
1988	1	15	1	2	
1989	1	12	2	2	
1990		34	2	1	
1991		15		1	
1992	1	9	3		
1993		27		2	
1994		14	2	3	
1995		9	1	3	
1996	1	35		2	
1997	2	12	1	1	
1998	1	17	1	2	
1999	1	34	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		high
2008	3	10			high
2009	2				high
total	40	596	55	79	