Estimated calf and perinatal mortality in western North Atlantic right whales (*Eubalaena glacialis*)

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ABSTRACT

Reduced reproductive success has contributed to lack of recovery of the endangered western North Atlantic right whale (*Eubalaena glacialis*). Here we examined the specific life history period from just before birth through the first year to estimate calf and perinatal losses between 1989 and 2003. The lower bound estimate (17 mortalities from 208 calving events) included documented calf mortalities and presumed deaths from serious injury or disappearance from the sighting record. The upper bound estimated potential calf losses from females with delayed first parturition (>10 yr) and shortened (2 yr) or lengthened (≥4 yr) calving intervals, if the female migrated to the calving ground during these intervals. Because cows were sighted in the calving ground predominantly in years when they were available to calve, adult females sighted there in a possible calving year without a calf were assumed to have experienced a perinatal loss. Twenty-eight potential perinatal losses were detected, bringing the upper bound of calf and perinatal mortality to 45 (3.0 calves/yr). The high frequency of lengthened calving intervals in *E. glacialis* suggests that abortion and neonatal losses are contributing to lower reproductive success compared to Southern Hemisphere right whales (*Eubalaena australis*).

Key words: reproduction, calf mortality, calving intervals, abortion, perinatal, neonatal, right whale, *Eubalaena glacialis*.

Despite protection since 1935, the western North Atlantic right whale population (*Eubalaena glacialis*) remains in peril, as it numbers less than 400 individuals (IWC 2001a, Hamilton *et al*. 2007). In addition to significant mortality from vessel collisions and fishing gear entanglements, a low reproductive rate has contributed to the lack of recovery in this species (Knowlton *et al*. 1994; Kraus *et al*. 2001, 2007). Almost 30 yr of repeated longitudinal sightings of identified females and their calving events (Kraus *et al*. 1986a, Hamilton *et al*. 2007) have revealed several indications of

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reproductive impairment. Yearly calf counts have been highly variable, ranging from 1 calf (in 2000) to 31 calves the following year (Kraus et al. 2007). Calf counts were significantly lower than expected by chance during two 3-yr periods (1993–1995 and 1998–2000) (Kraus et al. 2007). These periods of low reproductive success coincided with an increased prevalence of skin lesions and a reduction in body condition scores based on visual assessments, however, the causes of these observations have not been determined (Pettis et al. 2004, Hamilton and Marx 2005). Both episodes of reduced calving were followed by a significant rebound in births, presumably due to recovery by individual females that were not calving during these intervals, indicating that a population-wide impact on reproduction had most likely occurred.

In addition, mean calving intervals (years between calves) for North Atlantic right whales have varied widely. The most frequently observed calving interval for Southern Hemisphere (Eubalaena australis) right whales is 3 yrs, including approximately: 1 yr of pregnancy; 1 yr in which birth, lactation, and weaning occurs; and 1 resting yr for replenishment of body condition (Best et al. 2001; Burnell 2001, 2008; Cooke et al. 2001). In contrast, mean calving intervals in North Atlantic right whales increased from about 3.5 yrs in 1990 to over 5 yrs from 1993 to 2003, then decreased abruptly to just over 3 yrs in 2004 and 2005 (Knowlton et al. 1994; Kraus et al. 2001, 2007). First observed parturition has been seen as early as 5 yrs old and as late as 21 yrs, with a mean of 10.1 yrs (Kraus et al. 2007), suggesting that delayed parturition is occurring in some cows either because of a failure to conceive, pregnancy loss, or undetected calf mortality. Unobserved calving events constitute another possible explanation, but seem less likely in this population because of long-term, intensive survey effort in the calving grounds along with the subsequent spring and summer feeding habitats (Brown et al. 2007).

Furthermore, through 2005 12% of mature females had never been sighted with a calf despite extensive surveys of the only known calving grounds in the southeastern United States (SEUS) (Kraus et al. 2007). These females ranged in age from 17 to >25 yrs old, well beyond the mean age of first parturition for this species. Combined, the periods of low calving, increased mean calving intervals, increased ages of first observed parturition, and the high proportion of nulliparous females point to reduced fecundity in this population compared to southern right whales. As a result, the reproductive rates in North Atlantic right whales have averaged one-third to one-half those of their Southern Hemisphere counterparts (Frasier et al. 2007, Kraus et al. 2007).

Kraus et al. (2007) proposed that the observed older age at first parturition and visitation of the calving grounds by mature females that are not sighted with a calf, could be indicators of late-term pregnancy loss or neonatal death. In addition, several authors have suggested that deviations from 3-yr calving intervals in right whales could indicate pregnancy loss (e.g., spontaneous abortion, stillbirth), or undetected calf deaths shortly after birth (i.e., neonatal losses; Knowlton et al. 1994, Burnell 2001, Cooke et al. 2001, Kraus et al. 2001, Elwen and Best 2004). Sighting data from several right whale populations provide some supporting evidence for this hypothesis. In the right whale calving ground off the Head of the Great Australian Bight, it is unusual to sight females in non-calving years. However, four of five females with 5-yr calving intervals were sighted in this area without calves in the third year, suggesting that these females had lost a calf at 3 yrs followed by a shortened 2-yr interval because they had skipped the depletion of body fat stores during lactation (Burnell 2001). Two-year calving intervals have been reported at a low frequency for right whale populations off Australia (Burnell 2008), South Africa.
Two-year intervals have been observed after documented early neonatal death, followed by ovulation after 1 yr (instead of 2 yrs), while 4-yr intervals have resulted from two successive calf losses (Burnell 2001).

Elwen and Best (2004) found that both 2- and 4-yr intervals occur more frequently in cows following the first calf than in more experienced cows (three or more calves), and concluded that these intervals indicated reproductive failure. North Atlantic right whales have a much higher frequency of lengthened calving intervals (≥4 yrs between calves) compared to southern right whales (Knowlton et al. 1994, Kraus et al. 2001). Knowlton et al. (1994) proposed that 4-yr calving intervals in North Atlantic right whales could be explained by loss of the fetus in early pregnancy before significant energetic costs were incurred by the mother during lactation, while later abortion or early calf loss might be seen as 5-yr intervals. Intervals longer than 5 yrs could be explained by combinations of these shorter intervals. There is no published record of a female right whale from any population calving in consecutive years.

In this paper, we explore the possibility that some of the shortened and the lengthened calving intervals, as well as the delayed first parturitions seen in North Atlantic right whales are indicators of pregnancy losses and undocumented neonatal mortalities, which have contributed to the low reproductive rates in this species. We do not attempt to examine all possible causes of the lengthened calving intervals and delayed first parturitions observed in this population (e.g., failure to conceive because of infertility of males or females, impacts of inbreeding depression or inadequate food resources). Rather we present both documented calf mortalities (death in the first 12 mos), and the potential contributions of pregnancy loss or undocumented neonatal deaths based upon the hypothesis (which we test) that mature females migrate to the SEUS predominantly in years in which they are available to calve because they are pregnant. We use sightings data for all reproductively viable females in the SEUS calving grounds to estimate these potential perinatal losses, including abortions, unobserved stillbirths and neonatal deaths. Finally, an updated comparison of calving intervals between Southern and Northern Hemisphere right whales is presented.

**Materials and Methods**

**Surveys and Sightings Data**

The only known calving ground of the North Atlantic right whale is off the southeastern United States (from Savannah, Georgia to St. Augustine, Florida) (Kraus et al. 1986a, Zani et al. 2008). Yearly aerial surveys of the right whale calving grounds were conducted on a limited basis from 1984 to 1987, and expanded from 1988 to 1993 by including systematic daily surveys in the core calving ground annually from December through March. In 1994, these surveys expanded spatially, and were conducted daily (weather permitting) from 1 December to 31 March and continue to the present (Brown et al. 2007). Because of the extensive survey effort in this area and the near-shore tendency of females with calves, most calving events have been documented (Kraus et al. 2007). In this study, sightings data from 1989 through 2003 were used because of relatively consistent survey effort during this time period and completion of the photo-identification data set.
Individual Whale Identification

All right whales sighted during aerial surveys were photographed, and individuals were subsequently identified by the pattern of callosities on the rostrum, lips, chin, and behind the blowholes, as well as scars on the head, body, and flukes (Payne et al. 1983, Kraus et al. 1986b, Hamilton et al. 2007). Right whale sightings were processed through the North Atlantic Right Whale Catalog, which contains all images and associated sightings data from 1935 to the present (Hamilton et al. 2007). The Catalog provided data on: calving events, annual calf counts, age at first observed parturition, and calving intervals (Kraus et al. 2007). For sightings in the calving ground, whales one-half or less of the body length of an associated adult were considered calves of the year. In northern feeding/nursery habitats, cow–calf pairs were confirmed by three separate sightings of the pair in close proximity or by observations of the pair through three consecutive dive cycles (Knowlton et al. 1994). All calves sighted between December and the following November were classified as being born in the same calving year (starting in January of that season).

Age and Reproductive Viability

Right whale ages were classified as follows: whales observed between birth and 1 yr were considered calves, those between 1 and 8 yrs were juveniles, and those at least 9 yrs of age were adults (Hamilton et al. 1998). Whales with an unknown birth date (i.e., not first seen as calves) were considered of unknown age until 8 yrs of subsequent sightings made them an adult (at least 9 yrs old). Females were classified as "reproductively viable" if they had calved at any point in their life history, and remained viable until a documented death or presumed death because of a 6-yr gap (or greater) in their sighting history (Knowlton et al. 1994, Hamilton et al. 2007). Determination of age, reproductive viability, and presumed death were informed by some data on individual whales that was collected outside of the 1989–2003 study period (e.g., if the first sighting of a whale occurred before 1989, or if a documented calving event occurred after 2003).

Lower Bound of Calf Mortality

The lower bound of calf mortality was estimated from three sources of data. The first data set included all dead calves for which a carcass was discovered (Moore et al. 2004, North Atlantic Right Whale Consortium2). The second data set included calves with a serious injury at the last sighting that probably resulted in death, using the wound and health criteria outlined by Knowlton and Kraus (2001), to determine probable death. The third data set included calves that were seen in the SEUS with their mother, but were not resighted after 1 May of the same year (between 2- and 6-mo-old depending on the birth date). These calves were presumed to be dead if the mother was sighted at least twice within the following six months without the calf (the calf was not presumed dead if the mother was not resighted after 1 May). The sighting history of those mothers in the following year was also examined to determine if the calf in question had been resighted.

Upper Bound of Calf Mortality

The upper bound of calf mortality included the lower bound plus estimation of “potentially lost calves,” including fetal and neonatal deaths. These inferred “potentially lost calves” were based on the premise that undetected fetal and neonatal mortalities (occurring during late pregnancy or shortly after birth) could be reflected by: (1) an increased age at first observed parturition (≥10 yrs old), or (2) a shortened (2 yr) or lengthened (≥4 yr) calving interval, and (3) migration by the individual females to the calving ground during these intervals. We calculated the upper bound estimate using the mean age of first parturition (≥10 yrs old) for these analyses, and included only reproductively viable females. The upper bound analyses were based on the hypothesis that reproductive females visited the calving ground predominantly in years in which they could potentially calve (i.e., were pregnant). In effect, we used the sightings data of mature females in the calving grounds to differentiate between delayed first parturitions and lengthened calving intervals potentially caused by perinatal losses vs. those resulting from other factors resulting in a failure to conceive (because the female would not be pregnant, she would not be expected to migrate to the calving ground). The null hypothesis was that there was no difference between sightings of reproductively viable females in the SEUS in years in which they are available to calve vs. not available to calve. To test this hypothesis, a Yates corrected chi-square was used to compare: (1) the number of females available to calve sighted in the SEUS, (2) the number of females available to calve that were not sighted in the SEUS, (3) the number of females not available to calve sighted in the SEUS, and (4) the number of females not available to calve that were not sighted in the SEUS. Differences were considered significant if $P < 0.05$.

Calving histories of reproductively viable females were examined to find cases with an increased age at first observed parturition, or a shortened or lengthened calving interval. Following Elwen and Best (2004) and Knowlton et al. (1994), this analysis assumed that shortened (2 yr) intervals indicated early calf loss followed by conception after 1 yr, and that lengthened (≥4 yr) calving intervals indicated fetal or neonatal loss followed by ovulation and conception the next year. Each female’s sighting history was analyzed to determine the years (between 1989 and 2003) in which she was potentially “available to calve,” and compared to the years in which she had been sighted in the SEUS calving grounds. Females were considered “available to calve” if: (1) they were 10 yr or older, or in the year of their first calving (if it occurred earlier); and (2) they were not classified as dead or presumed dead. Females were counted as “available” in all years of documented calving events. A female was not considered “available” in the year before a documented calving event as she would have been pregnant, nor in the 2 yr following a successful calving year, as she would be lactating in the first year, and replenishing body condition in the second year. The female was again “available” to calve in the third year after calving, and remained so until the year before the next documented calving event. Because 2-yr calving intervals have been observed in this population and in southern right whales following early calf mortality (Burnell 2001), if a female was known to have lost a calf within a few months of birth, she became “available” again in the second year.

To estimate the potentially lost calves indicated by an increased age at first observed parturition, the SEUS sighting histories of reproductively viable females at least 10 yrs old (mean age at first observed parturition) were examined. Each year in which a female was sighted in the SEUS between age 10 and the first documented calving was counted as one potentially lost calf, except for observations made in the year
before a known calving event (i.e., she was known to be pregnant), and cases in which a female was sighted in the SEUS 2 yr in a row. The latter situation was counted as only one potentially lost calf, as consecutive year calving has never been documented in right whales. If a female was not sighted in the SEUS in any years between age 10 and the first documented calving, then she did not contribute any potentially lost calves to this analysis.

To estimate the potentially lost calves indicated by shortened or lengthened calving intervals, all SEUS sightings of available multiparous females with 2-yr and ≥4-yr calving intervals were examined. Calving intervals were determined using some data collected outside the study period, but only intervals that either partially overlapped (i.e., 1986–1991) or were entirely within the study period were utilized. For lengthened calving intervals, each nonconsecutive year an available female was sighted in the SEUS was counted as one potentially lost calf. In cases of especially long calving intervals (≥7 yr), only females with no sighting gaps longer than two consecutive years were included. The continuity in the sighting record decreased the possibility of missing a successful calving event during the lengthened calving interval. All potentially lost calves were screened against the database of documented mortalities (Moore et al. 2004, North Atlantic Right Whale Consortium) to verify that these deaths were unaccounted for in the lower bound figures (i.e., were not in the list of known calf mortalities).

Finally, we present an updated comparison of the frequency of different length calving intervals in Northern and Southern Hemisphere right whales. The southern right whale data was from southern Australia for the period 1996–2007 (Burnell 2008) and South Africa for the period 1979–2000. The North Atlantic right whale data included only calving intervals occurring within the study period (1989–2003).

While most calving events are documented for the North Atlantic right whale population because of a small population size and extensive annual survey efforts in several habitats (Kraus et al. 2007), it is important to note that the data from the Southern Hemisphere right whales is based upon observed calvings on the winter calving grounds only, and is uncorrected for missed calving events.

RESULTS

Our analyses included the calving history and sightings data for 112 female North Atlantic right whales, including a total of 208 documented calving events. During this study, 101 of the 112 females calved, and 65 of these calved multiple times. A total of three shortened and 114 lengthened calving intervals were analyzed for this study.

Lower Bound of Calf Mortality

A total of 17 calves were known to have died or were presumed dead between 1989 and 2003 (Table 1). Fifteen of these were documented mortalities in which 11 carcasses were recovered for necropsy, and four were not recovered. Two additional calves were presumed dead, one due to a serious injury at the last sighting, and the second because of its disappearance despite multiple resightings of the mother.

3Personal communication from Peter Best, MRI Whale Unit, South African Museum, P. O. Box 61, Cape Town 8000, South Africa, January 2008.
Table 1. Documented North Atlantic right whale calf mortality and calves presumed to be dead (1989–2003).

<table>
<thead>
<tr>
<th>Status</th>
<th>Calf of right whale number</th>
<th>Date carcass first sighted/calf last sighted alive</th>
<th>Location of carcass/sighting</th>
<th>Cause of deatha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>3 January 1989</td>
<td>Georgia</td>
<td>Live stranded/ probable perinatal</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>26 January 1989</td>
<td>Florida</td>
<td>Undetermined</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>8 September 1989</td>
<td>Florida</td>
<td>Undetermined</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>5 January 1993</td>
<td>Florida</td>
<td>Vessel collision</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>15 January 1993</td>
<td>Florida</td>
<td>Undetermined    (perinatal?)</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>2 January 1996</td>
<td>Florida</td>
<td>Undetermined</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>19 February 1996</td>
<td>Georgia</td>
<td>Undetermined</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>22 February 1996</td>
<td>Florida</td>
<td>Undetermined</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>9 January 1997</td>
<td>Florida</td>
<td>Perinatal-complication during birth?</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>10 January 1998</td>
<td>Georgia</td>
<td>Perinatal-stillborn</td>
</tr>
<tr>
<td>Dead</td>
<td>1303</td>
<td>13 February 2001</td>
<td>Florida</td>
<td>Undetermined</td>
</tr>
<tr>
<td>Dead</td>
<td>2123</td>
<td>17 March 2001</td>
<td>Virginia</td>
<td>Vessel collision</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>18 June 2001</td>
<td>New York</td>
<td>Vessel collision</td>
</tr>
<tr>
<td>Dead</td>
<td>Unknown</td>
<td>10 June 2002</td>
<td>Massachusetts</td>
<td>Vessel collision</td>
</tr>
<tr>
<td>Presumed dead</td>
<td>1004</td>
<td>23 February 1994</td>
<td>N/A</td>
<td>Significant wound to flukesb</td>
</tr>
<tr>
<td>Presumed dead</td>
<td>1812</td>
<td>17 March 2002</td>
<td>N/A</td>
<td>Undeterminedc</td>
</tr>
</tbody>
</table>

aFrom Moore et al. (2004).

bThe 1994 calf of right whale no. 1004 was sighted with deep lacerations on the head, lip region and on both sides of the dorsal flukes. The flukes were not functional at last sighting.

cRight whale no. 1812 was sighted without her calf on two separate occasions (3 and 14 June 2002), within 5 months of birth.

The number of documented mortalities per year varied from 0 to 4, with a mean of 1.1 calves/yr (SD = 1.2). Over the entire study period, 8% of the documented calves died or were presumed dead (the yearly range was 0%–25% of annual calf production).

Available to Calve and Migration to the Calving Ground

Of 228 sightings of 112 mature females in the SEUS during the study period, 210 were available to calve the year they were sighted and 18 were not available (Table 2). Females seen in the SEUS were significantly more likely to be available to calve than not (Yates corrected $\chi^2 = 156.67, df = 1, P$ (two-tailed) < 0.0001), thus rejecting the null hypothesis. Of the 18 sightings of nonavailable females in the SEUS, 10 were seen with their offspring from the previous calving season and three were sighted in the year prior to a documented calving (i.e., pregnant). The remaining five females were unavailable because they had successfully calved in the
Table 2. Sighting data (1989–2003) for females in years in which they were available to calve (or not), and whether (or not) they were sighted in the SEUS calving grounds. There was a highly significant association between being available to calve in a given year and being sighted in the SEUS ($P < 0.0001$).

<table>
<thead>
<tr>
<th>Female status</th>
<th>No. of sighted in SEUS</th>
<th>No. of not sighted in SEUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Available to calve</td>
<td>210</td>
<td>395</td>
</tr>
<tr>
<td>Not available to calve</td>
<td>18</td>
<td>473</td>
</tr>
</tbody>
</table>

previous year or two. However, not all calving females were sighted in the SEUS calving ground. A total of 172 of the 208 calves (83%) born during the study period were first sighted in the SEUS, while the other 17% (36/208) were first observed in other habitat areas.

**Upper Bound of Calf Mortality**

The analyses for the upper bound of calf mortality yielded an additional 28 potentially lost calves, bringing the total, including the lower bound ($n = 17$), to 45 (3.0 calves/yr). Twelve of these, from 10 different females, were potentially missed first calving events (*i.e.*, females of at least 10 yrs of age who were sighted in the southeast calving ground without a calf). The remaining 16 potential calf losses, from 13 females, were detected from lengthened calving intervals of available females that were seen in the SEUS calving ground (Table 3). Available females were sighted in the calving ground during 14.0% (16/114) of the lengthened calving intervals examined in this study (Table 3). Although three females were identified with a 2-yr calving interval, each of the calves lost prior to the shortened intervals were known mortalities and thus were included in the lower bound of calf mortality.

Table 3. Potentially lost calves estimated from lengthened calving intervals (≥4 yr) and sightings of “available” females in the SEUS calving ground (1989–2003).

<table>
<thead>
<tr>
<th>Calving interval (yr)</th>
<th>Total number of lengthened calving intervals</th>
<th>No. of “available” females sighted in SEUS during interval</th>
<th>No. of potentially lost calves</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>31</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>33</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>21</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>7</td>
<td>13</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>8</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>11</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>1’</td>
<td>2</td>
</tr>
<tr>
<td>13</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>1</td>
<td>1’</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>114</td>
<td>13</td>
<td>16</td>
</tr>
</tbody>
</table>

*Note:* The asterisks indicate females that potentially lost multiple calves.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total number of calves born</th>
<th>Live calves</th>
<th>Known/presumed calf mortalities</th>
<th>Estimated calf/perinatal mortality</th>
<th>Total no. of calves born + estimated calf/perinatal mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>18</td>
<td>16</td>
<td>2</td>
<td>4</td>
<td>22</td>
</tr>
<tr>
<td>1990</td>
<td>13</td>
<td>12</td>
<td>1</td>
<td>1</td>
<td>14</td>
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<td>1991</td>
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<td>3</td>
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<td>1</td>
<td>20</td>
</tr>
<tr>
<td>Total</td>
<td>208</td>
<td>191</td>
<td>17</td>
<td>28</td>
<td>236</td>
</tr>
</tbody>
</table>

During the study period, a total of 208 calves ($\bar{x} = 13.9$ calves/yr, SD = 8.2) were born, and 191 of these survived through their first year. If known calf mortalities, potentially lost calves, and surviving calves are combined, a total of 236 calves ($\bar{x} = 15.7$ calves/yr, SD = 9.0) would have been born during this period (Table 4).

Calving Intervals in Northern and Southern Hemisphere Right Whales

Table 5 summarizes the reported frequency of different length calving intervals for the North Atlantic, southern Australian and South African right whale populations.

Table 5. Calving interval frequencies in Northern and Southern Hemisphere right whale populations.

<table>
<thead>
<tr>
<th>Population</th>
<th>Years</th>
<th>No. of calving intervals ($n$) and percentage of total (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Australia(^{a})</td>
<td>1996–2007</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2%</td>
</tr>
<tr>
<td>South Africa(^{b})</td>
<td>1979–2000</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2%</td>
</tr>
<tr>
<td>North Atlantic(^{c})</td>
<td>1989–2003</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2%</td>
</tr>
</tbody>
</table>

\(^{a}\)From Burnell (2008).  
\(^{b}\)Personal communication from Peter Best, MRI Whale Unit, ′/′, South African Museum, P. O. Box 61, Cape Town 8000, South Africa, January 2008.  
\(^{c}\)From Kraus et al. (2007).
The most frequently observed calving interval in Australian (65%) and South African (67%) right whales was 3 yrs. In contrast, 5-yr intervals were the most common (27%) for North Atlantic right whales, followed in frequency by 3-yr intervals (21%). Shortened calving intervals (2 yr) were reported in all three populations at the same frequency (2%). North Atlantic right whales showed a much higher occurrence of all calving intervals $\geq 4$ yr (78%) compared to both the Australian (33%) and South African (31%) populations.

**DISCUSSION**

Conservation efforts for the North Atlantic right whale have primarily focused on reducing the anthropogenic sources of mortality (Kraus et al. 2005, Kraus and Rolland 2007). However, comparatively little attention has been paid to the consequences of impaired reproduction on population recovery. The North Atlantic right whale population has been growing at rates of $-0.02\%$ (Fujiwara and Caswell 2001) to 2.5\% (Knowlton et al. 1994), significantly lower than right whales off South Africa (7.2\%), Australia (8.2\%), and Argentina (7.1\%) (IWC 2001b, Table 4). While some of this difference is certainly due to very high anthropogenic mortality rates in the North Atlantic, overall low calf production and extreme variability in annual calving rates (Kraus et al. 2007) suggests that impaired reproduction is also responsible.

Our hypothesis that reproductively viable, adult females rarely travel to the SEUS calving ground unless pregnant was supported by a strong association between being available to calve and being sighted in the SEUS (Table 2). Adult females have been observed on the SEUS calving ground in the year prior to calving and while accompanying their offspring from previous calving seasons. In these cases, the females were not available to calve. As there is no evidence of feeding in the SEUS, and mating behavior is more commonly observed in the northern habitats, there are no known reasons for reproductively available females to expend the energy to travel to the SEUS calving ground other than pregnancy.

The upper bound of potentially lost calves described in this paper undoubtedly underestimates reproductive failure in the North Atlantic right whale population for several reasons. First, the number of documented calves born per year includes calves sighted in all habitats, not just those sighted in the SEUS. Of the 208 calving events documented during the study period, 17\% were observed only in the northern habitats. Because survey effort is far less comprehensive in those areas, calf loss for females that did not travel to the SEUS could not be estimated. Second, the mean age of first calving (10 yr) was used to estimate the number of calves potentially lost before the first documented calving. The age of sexual maturity in right whale females has been defined by calving events, and undetected calves lost prior to the first observed calving could have increased the estimated mean age of sexual maturity. Because right whales have had calves as early as age 5 (Knowlton et al. 1994), travel to the SEUS by females under the age of 10 probably represented some additional lost calves. If age 5 were used in the analysis instead of age 10, the total number of lost calves would increase from 45 (3.0 calves/yr) to 76 (5.1 calves/yr). Third, in the absence of comprehensive hormone work on “available” females, there is no method for determining early pregnancy loss. Females that conceive and then abort early in the pregnancy may not migrate to the SEUS, and those events would not be counted as potential calf losses. Fourth, more limited aerial survey effort in the calving ground in the early years of this study (1989–1993) could have contributed to an
underestimation of the potential calf losses because of missed sightings of females that were available to calve. Finally, nulliparous females comprised approximately 10% of the adult females (12/124) in this population during the study period (1989–2003), but were not included in this analysis because they were not known to be reproductively viable. However, 11 of the 12 identified nulliparous females were sighted in the SEUS as adults (ages ranged from 10 to at least 20 yrs old), suggesting that they may have conceived and then lost calves in the years they traveled to the calving grounds.

Conversely, potential calf loss could have been overestimated if some females became sexually mature after age 10. If these females were not reproductively mature when sighted in the SEUS, their presence there could perhaps be attributed to exploration of the calving ground. In addition, lengthened calving intervals may not always represent an aborted pregnancy or neonatal death, even when the female travels to the SEUS. Burnell (2001) suggested that some females may calve normally at a 4-yr interval, due to the high proportion of such intervals in the Australian population (Table 5). Finally, from the sighting records of known cow–calf pairs and documented calf mortalities, eight dead calves were identified that could not be assigned to any of the known cows in this study. It is possible that these dead calves may be duplicates of some of the “potentially lost calves” that were identified in the upper bound analysis.

Several potential causes of abortion and neonatal death have been identified in cetaceans. Infectious diseases known to cause spontaneous abortions in domestic animals, such as brucellosis and leptospirosis, have been documented in cetaceans (Smith et al. 1974, Miller et al. 1999, Kraus et al. 2007). Scholin et al. (2000) associated domoic acid, a marine biotoxin, with fetal and neonatal deaths in California sea lions (Zalophus californianus). Both domoic acid and PSP toxins (paralytic shellfish poisoning) have been found in North Atlantic right whales (Doucette et al. 2006, Rolland et al. 2007). Genetic factors can also play a role in causing abortions and neonatal death. Frasier et al. (2007) reported that matings were only successful between genetically dissimilar individuals and suggests that the low level of genetic variability in right whales could be increasing the occurrence of unsuccessful pregnancies (and conceptions). Although not well studied in right whales, contaminants present in the marine environment have been shown to interfere with reproduction and development in wildlife through disruption of endocrine pathways (Colborn et al. 1993), and some of these chemicals have been found in other marine mammals (DeBoer et al. 1995, Kajiwara et al. 2006, Ross et al. 2009).

Climatic changes may also impact calving success by changing the availability of prey. Leaper et al. (2006) reported a relationship between global climate signals and interannual variability in calving success in southern right whales. Studies by Kenney (2007) and Greene and Pershing (2003) found evidence of an association between climate variability and calving rates in North Atlantic right whales. A diminished food supply in years of body replenishment and pregnancy could reduce successful conceptions and calving, given the high energetic expense of reproduction (Kraus et al. 2007). Food limitation could also contribute to calf deaths between birth and weaning as a female with diminished body condition may not be able to sustain the high energetic cost of lactation.

These analyses indicate that undetected calf mortality and perinatal losses are contributing to low reproductive success in North Atlantic right whales. However, delayed or failed conceptions and early pregnancy losses (in which females do not migrate to the SEUS) are undoubtedly also important causal factors. In fact, available
females were sighted in the calving grounds during only 14% (16/114) of lengthened calving intervals (≥4 yr). Therefore, in the majority of cases, the failure to calve in a potentially available year was most likely due to conception failure, delayed conception or early pregnancy loss. Furthermore, while our analyses showed that mature females seen in the SEUS were significantly more likely to be available to calve than not, the majority of females available to calve (n = 395) did not travel to the SEUS (Table 2), suggesting that they did not become pregnant, or lost the pregnancy early.

Elwen and Best (2004) used observed calving intervals of individual females as an index of reproductive success. In their study, 3 yr intervals were considered successful, while 2- and 4-yr intervals indicated unsuccessful reproduction. For the period 1989–2003, 77% of calving intervals in the North Atlantic population were ≥4 yr with only 21% of intervals occurring at 3 yr (Table 5). Intrinsic differences between Northern and Southern Hemisphere right whales may explain this contrast in calving interval frequencies. However, the North Atlantic data was heavily weighted by the period 1993–2003, during which the mean calving interval increased to over 5 yr for unknown reasons (Kraus et al. 2007). If the yearly calving interval data is analyzed eliminating the period 1993–2003, 61% of calving intervals occurred at 3 yrs, a much closer approximation of southern right whale intervals. Therefore, the much higher frequency of lengthened calving intervals in North Atlantic vs. Southern Hemisphere right whales most likely indicates that abortions, neonatal deaths, and unsuccessful or delayed conceptions have been more frequent in the North Atlantic population.

More research on reproduction in this species is urgently needed. As this study has shown, documenting lone females in the SEUS may be as informative as documenting of cow–calf pairs in regards to reproductive success. Rolland et al.’s (2005) methods for assessing hormone metabolites in right whale fecal samples to detect pregnancies could be used to confirm pregnancy loss in females that are sighted in the calving ground without a calf. The effects of inbreeding and climate change on right whale reproduction also need further attention. Finally, it is likely that North Atlantic right whale reproduction is influenced by the cumulative impacts of coastal industrialization of the east coast of the United States and Canada (Kraus and Rolland 2007b). The long-term survival of right whales depends upon their ability to reproduce, and that may depend upon the identification and reduction of the specific and cumulative impacts of human activities.

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