Reproductive parameters of the North Atlantic right whale

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ABSTRACT

North Atlantic right whale reproduction was assessed for the period 1980 through 1998. At the end of this period, we estimated there were between 299 and 437 right whales alive, including 70 mature females. Using maximum and minimum population estimates for the entire period, mean values for gross annual reproductive rate were 0.36 and 0.49 respectively, and the mean value for calves per mature female per year was 0.25. There is a significant decreasing trend in calves per mature female per year over the entire study period. The mean age at first calving is 9.53 years. The mean number of cows recruited annually since 1985 is 3.8. Mean annual calving intervals have increased significantly during the study period from 3.67 years (1980-1992) to over 5 years (1993-1998). Although the North Atlantic population is affected by significant anthropogenic mortality, diminishing reproductive rates are probably also responsible for the plight of this species.

KEYWORDS: REPRODUCTION; TRENDS; RIGHT WHALE; NORTH ATLANTIC

INTRODUCTION

The North Atlantic right whale (Eubalaena glacialis) is the rarest species of large whale in the world (Brownell et al., 1986). Despite protection for over 60 years, estimates of current abundance for this species indicate that only about 300 animals survive today (Knowlton et al., 1994; IWC, 2001). Contemporary studies show low levels of recovery, and many years of data are being examined to assess the potential problems in this population. The photographic identification of individual whales has proved to be invaluable in evaluating a variety of life-history parameters for the North Atlantic population, including: sex ratios; birth and death rates; inter-birth intervals; and population abundance and trends (e.g. Kraus et al., 1986a; b; Fairfield, 1990; Hamilton and Mayo, 1990; Kraus, 1990; Kenney and Kraus, 1993; Schaeff et al., 1993; Brown et al., 1994; Knowlton et al., 1994; Hamilton et al., 1995; 1998; Caswell et al., 1999).

Knowlton et al. (1994) summarised the then available information on reproductive biology of the western North Atlantic right whale population based on data obtained by repeated sightings of photographically identified individuals. From 1980-1992, 145 calves were born to 65 different females. Mean age at first birth was 7.57 years, which was expected to increase with the duration of the study. The number of reproductively active females was stable at around 51 animals from 1987-1992, with newly mature recruits balancing mortalities. The mean interval between calves was estimated at 3.67 years. Although the data suggested that this interval was increasing with time, the trend was not statistically significant. The total number of individuals in the population was estimated at 295. Gross annual reproductive rate (GARR), mortality rate and population growth rate were estimated at 4.5%, 2.0% and 2.5%, respectively. The population growth rate was substantially lower than southern right whale populations off Argentina and South Africa (Best, 1990; Payne et al., 1990). Anthropogenic mortality caused by collisions with ships and entanglement in fishing gear were identified as among the primary causes of poor population recovery. However, other potential problems were suggested as factors that may lead to reduced reproductive rates, including inbreeding depression, competition for food from other species, climatic changes resulting in reduced food availability and sub-lethal effects of toxic contaminants. Since Knowlton et al. (1994), additional information has become available and some parameters have changed. An updated analysis is presented of North Atlantic right whale life history parameters, including data collected through 1998 which suggest that reproduction has recently been compromised.

METHODS

Right whales in the North Atlantic have been individually identified and catalogued since the 1950s using the callosity patterns and scars found on their heads and bodies (Payne et al., 1983; Kraus et al., 1986a). Right whale identification photographs have been obtained through both aerial and shipboard surveys over the last twenty years. Although there has been significant variation in effort from year to year, photographic surveys for right whales have been undertaken annually in the southeastern US wintering ground since 1984, in Cape Cod Bay since 1982 and in the Bay of Fundy since 1980. Right whale surveys started in the Great South Channel in 1979, but there have been several years in the early 1990s with no effort in that area. Surveys on the Nova Scotian Shelf started in 1983, and have continued sporadically to the present. Since photographic identifications provided repeated records of individual whales, information on population size, mortality and reproductive parameters (including annual calf production, calving intervals, age at first parturition and the number of new cows recruited annually) was available from the North Atlantic right whale catalogue (Hamilton and Martin, 1999). A supplementary genetics study has provided gender information for 270 individuals (Brown et al., 1994). Subsets of the data were used to examine different questions.

In the present paper, population estimates were obtained in two ways. The total catalogued population minus the cumulative numbers of presumed dead¹ for that year was chosen as a lower estimate (Table 1, \( n_{\min} = i - n_{\bar{p}} \)). This

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¹ New England Aquarium, Boston, MA 02110, USA.
² University of Rhode Island, Graduate School of Oceanography, Narragansett, RI 02882, USA.
³ i.e. Not seen for five years following Knowlton et al. (1994), and see below.
estimate is likely to be low, since not all calves are photographically identified in a given year, and some animals presumed dead may be re-sighted after a five year gap in the sighting record. The second estimate (Table 1, \( n_{\text{max}} \)) was obtained using the back-calculating method of Knowlton et al. (1994) for the entire period, but assuming zero presumed mortalities. The starting year was 1998 as all catalogued whales minus those known to be dead plus all calves known to be born but not photographically identified \((n = 53)\). Previous years were then estimated by subtracting the calves of year \( x \) for year \( x - 5 \), and adding any mortalities known to have occurred in the catalogued whales in that year (known mortalities are given in brackets in Table 1 under catalogued whales). Since additional unreported mortality probably occurred, and some calves not identified in their first year may have been added to the catalogued whales at a later date, these estimates are considered to be too high.

Right whale mortality was documented through strandings, although not all dead animals are reported or come ashore. Mortality was therefore estimated for the population by presuming death in the sixth year for any individual with a hiatus of five years or more in the sighting records (Table 1, \( m_p \)). Where dead stranded right whales were identified \((n = 10)\), those individuals (identified in brackets) were removed from the cumulative count of catalogued whales (Table 1, \( i \)) in the year in which they died. Prior to 1986, the study period was not long enough to meet the presumed dead criterion, so the early \((m_p)\) estimates are unreliable. After 1992, offshore survey effort in the Great South Channel and the Nova Scotian Shelf was reduced. It is believed that not all whales presumed dead in this period were really dead – they may just be missing from the limited photographic samples.

For estimating reproductive parameters, adult females were classified as mature beginning in the year in which they were first seen with a calf, and were eliminated from all subsequent counts if they died or were presumed dead after a six-year hiatus in sightings. GARR was estimated from the number of calves expressed as a proportion of the total estimated population for both the lower and upper abundance estimates. Calves per mature female per year (CMFY) was estimated from the number of calves expressed as a proportion of the total number of mature adult females in that year.

All data on calving were used to estimate age at first parturition. New cows were counted as recruited to the population using data starting in 1985, to try and eliminate recruits who were in fact older cows that had not been observed with calves during the early part of the study period.

Annual calf production is presented for the years 1980-1998. We believe most calves have been reported in this population since 1991 because of intensive survey effort (ca. 90 aerial survey days per year) in the only known calving ground off the southeastern US in the winter. However, reliable photo-identification requires that young right whales have fully developed callosity patterns which in fact do not stabilise until they are six months old. Since all cows do not use the same summering habitats, not all calves are photographed between 6 and 12 months, and these therefore remain unidentified. Whales added to the catalogue as animals of unknown age probably represent unidentified calves that grew up without being sighted or clearly photographed in their first year rather than animals from an un-photographed population of adults. For this paper, annual calf count (Table 1, \( c \)) includes all calves, even those that

### Table 1

| Year | Catalogued whales \( (l) \) | Presumed dead \( (m_p) \) | Abundance \( \left( \frac{c}{n_{\text{max}}} \right) \) | Mature females \( \left( \frac{c}{n_{\text{max}}} \right) \) | Calves \( c \) | GARR \( \left( \frac{c}{m_p} \right) \) | CMFY \( \left( \frac{c}{n_{\text{max}}} \right) \) |
|------|----------------|----------------|-----------------------|-----------------------|----------------|-----------------|----------------|
| 1980 | 96 | 2 | 94 | 240 | 17 | 6 | 0.064 | 0.025 | 0.35 |
| 1981 | 149 | 4 | 145 | 246 | 21 | 8 | 0.055 | 0.033 | 0.38 |
| 1982 | 173 | 5 | 168 | 254 | 28 | 12(1) | 0.071 | 0.047 | 0.43 |
| 1983 | 189(1) | 5 | 184 | 265 | 34 | 9 | 0.049 | 0.034 | 0.26 |
| 1984 | 203 | 5 | 198 | 273 | 39 | 12 | 0.061 | 0.044 | 0.31 |
| 1985 | 220 | 5 | 215 | 285 | 41 | 11 | 0.051 | 0.039 | 0.27 |
| 1986 | 242(1) | 7 | 237 | 296 | 47 | 13 | 0.055 | 0.044 | 0.28 |
| 1987 | 258 | 9 | 249 | 308 | 51 | 11 | 0.044 | 0.036 | 0.22 |
| 1988 | 277 | 13 | 264 | 319 | 53 | 8(1) | 0.030 | 0.025 | 0.15 |
| 1989 | 297(1) | 19 | 276 | 326 | 52 | 18(2) | 0.065 | 0.055 | 0.35 |
| 1990 | 308 | 20 | 288 | 341 | 54 | 13(1) | 0.045 | 0.038 | 0.24 |
| 1991 | 321(1) | 28 | 293 | 353 | 54 | 17 | 0.058 | 0.048 | 0.31 |
| 1992 | 333(1) | 32 | 301 | 369 | 55 | 12 | 0.040 | 0.033 | 0.22 |
| 1993 | 343 | 34 | 309 | 380 | 57 | 8(2) | 0.026 | 0.021 | 0.14 |
| 1994 | 357 | 48 | 309 | 386 | 60 | 9 | 0.029 | 0.023 | 0.15 |
| 1995 | 364(2) | 62 | 302 | 395 | 60 | 7 | 0.023 | 0.018 | 0.12 |
| 1996 | 377(1) | 72 | 305 | 400 | 70 | 22(1) | 0.072 | 0.055 | 0.31 |
| 1997 | 390(1) | 77 | 313 | 419 | 75 | 20(1) | 0.064 | 0.048 | 0.27 |
| 1998 | 389 | 90 | 299 | 437 | 70 | 6(1) | 0.020 | 0.014 | 0.09 |

1 Includes all whales cumulatively identified in the North Atlantic up to and including that year, minus ten whales known to have died during the period \( (l) \). Known mortalities are given in brackets. 2 Includes all animals cumulatively presumed dead in that year \( (m_p) \). 3 Minimum population size \( n_{\text{max}} \) equals the total number of catalogued whales minus presumed dead for that year \( (l-m_p) \). Maximum population size \( n_{\text{max}} \) is back-calculated following the method of Knowlton et al. (1994), but in this case assuming zero presumed mortality. 4 Includes those observed at least once with a calf, minus those presumed dead. 5 Includes unidentified individuals (known deaths are in brackets). 6 GARR (gross annual reproductive rate or crude birth rate) is the number of calves expressed as a proportion of the total estimated population for both estimates. 7 CMFY (calves per mature female per year) is the number of calves expressed as a proportion of the number of adult females recorded as mothers in that or in any previous year.
remained unidentified (but whose mothers were recorded) and those that were known to have died in their first year (known calf mortalities are given in brackets in Table 1).

Calving intervals were examined for every cow in the population who calved more than once. Mean calving intervals were calculated from the annual totals, with intervals longer than seven years excluded because of gaps in the sighting records. Because of the possibility that females are calving in one or more unknown locations, and to examine whether the probability of sighting mature females had declined, the rate at which mature females were sighted annually throughout the study period was analysed. The intervals between sightings of both juvenile and mature females for the 1980s and the 1990s were also compared to see if there were differences in sighting probability. Finally, the sightings histories of mature females with six- or seven-year calving intervals were evaluated to determine whether the longer calving intervals could have included a missed calving record due to a reduced number of sightings prior to calving. To achieve this, it was assumed that no cow had a calf within the first two years of calving or within two years prior to calving. This assumption is based upon the low probability of a two-year calving interval. Of 127 calving intervals recorded since 1980, only one (less than 1%) was two years. Therefore, in this analysis of sighting histories, it was assumed that calves could have been missed in our database if cows were not observed in years three and four of a seven-year interval, or year three of a six year interval.

RESULTS

Estimates of population size and mortality

The population size in 1998 was estimated to be at least 299 and no more than 437 (Table 1). The current catalogue includes all known photographs of members of this population since 1935, and currently includes documentation of 389 individual right whales, ten of which are known to have died (Table 1, i) (Hamilton and Martin, 1999). The number of whales included in the catalogue at any one time does not represent an absolute count of North Atlantic right whales. The actual number may be lower (since unreported mortality is certain to occur) or higher (because not all calves born in any year are photographically identified). Between two and 14 animals were presumed to have died annually using the presumed mortality criterion, and the cumulative ‘presumed dead’ estimates are given in Table 1 by year. An additional negative bias is that there may be individual animals which are not approachable or which rarely or never use habitats where photographic sampling occurs, and therefore have never been photographed. Prior to the present paper and the consideration of abundance estimates given in IWC (2001), the only other published estimate is that of Knowlton et al. (1994). As noted in IWC (2001) recapture heterogeneity and changes in survey effort make capture-recapture estimates of abundance problematic.

Reproductive females

The number of reproductively active females has increased slowly throughout the study period, although it remained stable in the low fifties, from 1987-1992. Of 21 photographed mothers in 1996, 10 were new mothers, 10 had calved previously and 1 remains to be identified. An additional 8 new females calved in 1997, bringing the total number of cows to 75, although presumed mortalities reduced this number to 70 in 1998 (Table 1).

Calving rate

The number of calves born per year from 1980-1998 ranged from 6-22, with a high level of inter-annual variability. The mean annual calving rate for 1980-1998 was 11.32 calves per year (SE = 1.09). The calving rate was well below the mean for three successive years with 8, 9 and 7 calves in 1993, 1994 and 1995, respectively. In 1996 and 1997, however, the number of calves increased to record highs of 22 and 20 respectively. In 1998, calf production fell to a record low of 6 calves.

Calving intervals

Apparent calving intervals (the number of years between observed calves) have increased across the population of repeatedly calving females since 1992 (Table 2). Knowlton et al. (1994) reported a mean calving interval of 3.67 years (SE = 0.11; n = 86; range = 2-7). The most frequently observed interval was three years, with 53 observations (61.6%). They also reported an apparent trend toward increasing intervals with time, though it was not statistically significant (p = 0.083). Since 1992, there have been 40 new observations of calving intervals added, including only three observations of a three-year interval, representing 7.5% of the total.

The mean calving interval for multiparous cows for 1996 and 1997 (n = 22) was 5.3 years. In the 1993-1998 period, two females gave birth after apparent gaps of 13 years, although these animals were not observed in many of the intervening years. Calving intervals in the two periods 1980-1992 and 1993-1998 are significantly different (Wilcoxon Rank Sum Test; P < 0.001) whether the two 13-year intervals are included or not (Fig. 1). The 13-year intervals were dropped from all subsequent analyses.

Non-parametric one-way ANOVA (Kruskal-Wallis Test) showed statistically significant variability in calving intervals between years (p < 0.001); but no significant inter-individual variability (p = 0.749). A bi-variate ANOVA (parametric), looking at effects of year and
An analysis of individuals shows that the longer calving intervals in 1997 and 1998 can be attributed to animals with long gaps in the sighting records (Table 5), making it possible that calves by those individuals were missed. For 21 females with calving intervals of six or seven years, 12 could have had calves that were missed in this study. Of the nine females with long calving intervals that had adequate sighting records to exclude missed calves, eight occurred in the 1990s. However, of the 21 females with long intervals, 19 appear to use the southeastern US as their only calving ground. The remaining two cows (No.1242 and No.1248) have only been seen in the summer with calves in the Gulf of Maine and their calving location is unknown. We believe that the consistent survey effort in the southeastern calving ground since 1990 renders it unlikely that cows would be missed in that area. Given that calving areas do not appear to be feeding areas, they are probably less subject than northern habitats to re-distribution of whales in poor food years. We therefore suspect that these longer calving intervals are real, and not artefacts of missed sightings in calving years.

Age at first parturition

Knowlton et al. (1994) reported a mean age at first calving of 7.57 years (SE = 0.63). Since 1992, an additional 12 known-age females have given birth for the first time, more than doubling the sample size. The mean age at first calving is now 9.53 years (SD = 2.32), consistent with those reported for the southern right whale (Best et al., 2001; Cooke et al., 2001).
Cow recruitment
Since 1985, there have been between 0 and 10 new cows recruited into the population annually (mean 3.8 per year). Although younger females recruited into the breeding pool in the 1990s might be expected to have longer calving intervals (as less-experienced foragers and mothers), the analyses of interval by year and individual suggest this is not the case.

Estimates of GARR
The mean estimates of GARR for the entire period are 0.036 for the lower estimate and 0.049 for the upper estimate. Annual GARR estimates range from 0.020-0.072 for the lower population estimates, and from 0.014-0.055 for the upper population estimates (Table 1). Linear regressions on both GARR estimates show no statistically significant trends.

CMFY
The mean number of calves per mature female per year (CMFY) for the period is 0.25 (SD = 0.094). The mean CMFY for the 1980s is 0.30 (SD = 0.077) and for the 1990s is 0.20 (SD = 0.078). The annual variation in CMFY values is high, ranging from 0.09-0.42. A linear regression shows that the CMFY has decreased over the study period (slope = -0.0109, p = 0.0004).

DISCUSSION
The application of capture-recapture models to estimate biological parameters for this population are made problematic by the cumulative effects of capture heterogeneity (especially calving females), changes in survey effort since the 1990s, and large shifts in spring and summer whale distribution during the study period (Kenney, 1994). The application of models used by Best and Underhill (1990), Payne et al. (1990), and Barlow (1990) are rendered impractical because many of the assumptions of these models are violated. In addition, if subsets of the population are used that meet the assumption requirements, sample sizes become extremely small, the confidence intervals around those estimates are consequently large and the estimates are unhelpful in a management context. A cumulative identification approach was therefore used to put upper and lower bounds on the estimates of population used in this paper. Estimates of the population prior to 1986 are likely to be underestimates, as survey effort was inconsistent in all areas, and animals were still being ‘discovered’ photographically at a fairly high rate. Insufficient survey effort and photographic discovery may also increase presumed mortalities by making capture probabilities lower for offshore survey areas. Further discussion of the question of estimating abundance and the ‘presumed mortality’ concept is given in IWC (2001).

Annual calf production shows large variability, ranging from 6-22 calves during the study period, around a mean of 11.3. The three years (1993-1995) in which calving dropped well below the mean, followed years in which the distribution of the population on its feeding grounds was anomalous. In 1992, right whales apparently did not use the Great South Channel feeding habitat, and did not appear in the Nova Scotian Shelf feeding habitat during the ‘expected’ seasons, based upon all survey data from the 1980s (Sutcliffe and Brodie, 1977; Kenney, 1994). From 1993-1998, right whales were rarely observed on the Nova Scotian Shelf feeding ground but somewhat larger numbers than expected were observed in the Bay of Fundy. However, the lack of survey effort in the Great South Channel from 1993-1997 means that nothing is known of right whale occurrence during that period there. Clearly, a female right whale must obtain sufficient energy from feeding to have a surplus over her own energetic needs stored for pregnancy and lactation. If right whales were forced to spend more time than usual in searching for appropriate foraging locations, then mature females may have had more difficulty inassimilating sufficient food.

One dramatic feature of North Atlantic right whale reproduction is the significant increase in calving intervals over the 19 year period of study. No definitive causes for the increase exist, and hypotheses currently being examined to account for it include inbreeding, pollutant effects and food limitations (IWC, 2001). Other possibilities include large numbers of senescent mothers and/or an unstable age structure, although the analysis conducted by Hamilton et al. (1998) of age structure in this population does not provide much support to either hypothesis.

Mean GARR estimates for the study period are 0.049 and 0.036, which bracket the estimate of 4.5% made by Knowlton et al. (1994). Data collection in the North Atlantic includes large portions of the year-round range of the population and thus GARR values may not be comparable to Southern Hemisphere estimates, where study areas are limited to wintering calving grounds where segregation is known to occur. GARR data from Argentina shows ratios of calves to the total population vary between 10% and nearly 60% (Payne et al., 1990). Patenaude and Baker (2001) report that the calf/total whale ratio in the Auckland Islands wintering grounds ranged from 9-14% during the 1995-1997 period. Since the GARR data do not reflect mortality information, it is not possible to estimate population growth rate from these estimates. Nevertheless, the data presented here suggest that reproductive rates in the North Atlantic population are currently less than one half the rates of comparable right whale populations in the Southern Hemisphere. The North Atlantic population is clearly suffering from significant anthropogenic mortality, but a diminishing reproductive output may be equally responsible for the plight of this species (IWC, 2001). Comparative studies using the Southern Hemisphere right whales as ‘controls’ provide one option for identifying the reproductive issues in the North Atlantic population (and see NMFS, 2000).

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