Reproductive parameters of the North Atlantic right whale

SCOTT D. KRAUS*, PHILIP K. HAMILTON*, ROBERT D. KENNEY+, AMY R. KNOWLTON* AND CHRISTOPHER K. SLAY*

Contact e-mail: skraus@neaq.org

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 dead[1] for that year was chosen as a lower estimate (Table 1, $n_{min} = i\text{-}m_p$). This

* *New England Aquarium, Boston, MA 02110, USA.*
+ *University of Rhode Island, Graduate School of Oceanography, Narragansett, RI 02882, USA.*
[1] 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_{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$_{(x\text{-}1)}$ 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

Estimated measures of reproduction by year for North Atlantic right whales.

Year	Catalogued whales (i) [1]	Presumed dead (m_p) [2]	Abundance [3]		Mature females [4]	Calves (c) [5]	GARR [6]		CMFY [7]
			(n_{min})	(n_{max})			($c/(n_{min})$)	(c/n_{max})	
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)	5	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(2)	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
			1980-1998 means and SDs				0.049 (0.017)	0.036 (0.012)	0.25 (0.094)

[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 (*i*). Known mortalities are given in brackets. [2] Includes all animals cumulatively presumed dead in that year (m_p). [3] Minimum population size (n_{min}) equals the total number of catalogued whales minus presumed dead for that year (i-m_p). Maximum population size (n_{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.

Table 2

Distribution of calving intervals by year for North Atlantic right whales. Mean intervals are calculated from annual totals, with intervals longer than 7 years excluded because of inconsistency in the sighting records.

	Calving intervals in years							
	2	3	4	5	6	7	8+	Mean interval
1980	-	1	-	-	-	-	-	3.0
1981	-	-	1	1	-	-	-	4.5
1982	-	1	-	1	-	-	-	4.0
1983	-	2	1	-	-	-	-	3.3
1984	-	7	-	-	-	-	-	3.0
1985	1	6	-	2	-	-	-	3.1
1986	-	5	2	-	-	-	-	3.3
1987	-	4	-	1	-	1	-	4.0
1988	-	2	1	1	1	-	-	4.2
1989	-	7	2	4	-	-	-	3.8
1990	-	7	1	1	1	-	-	3.6
1991	-	4	3	3	2	1	-	4.5
1992	-	7	1	-	1	-	-	3.4
1993	-	-	3	1	-	-	-	4.3
1994	-	-	3	1	-	-	-	4.3
1995	-	1	1	1	1	-	1(13yr)	4.5
1996	-	-	1	6	2	1	-	5.3
1997	-	2	1	2	3	3	1(13yr)	5.4
1998	-	-	1	-	3	1	-	5.8
Totals	1	56	22	25	14	7	2	

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.

A 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

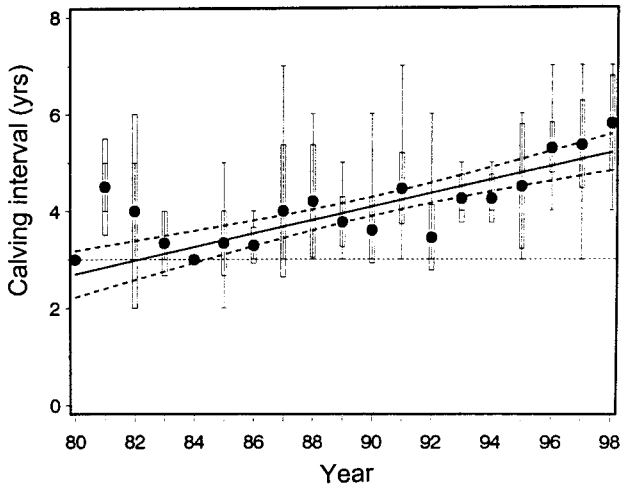

Fig. 1. Trends in calving intervals in the western North Atlantic right whale population, 1980-98. For each year, the mean is shown as a solid circle, one standard error to each side of the mean with a vertical box, and the range by a vertical line with a small horizontal tick at each end. The solid sloping line is the increasing trend shown by least-squares regression on all individual data points ($n = 127$), with the 95% confidence interval shown by dashed lines. The fine dashed line shows the 'typical' three-year interval expected in right whales for reference.

individual on calving intervals, showed that changes were statistically significant by year but not by individual cow ($n = 120$; YEAR: $F = 3.11$; $p < 0.001$; $n = 120$; INDIVIDUAL: $F = 0.67$; $P = 0.930$).

Linear regression analyses of trends in calving interval over time demonstrate that calving intervals have been increasing significantly between 1985 and 1998 (slope = 0.209; $n = 112$; SE = 0.037; $p < 0.001$). To determine whether changes in sighting rates of adult females could be affecting apparent calving intervals, sighting rates for mature females (those seen in a given year as a proportion of those available to be seen) were calculated. They have not changed significantly in 19 years, although there has been a slight increase over the period (Table 3).

A comparison of sighting intervals between the 1980s and 1990s for both juvenile and adult females shows no significant difference between the decades (Table 4).

Table 3

Sighting rate for adult females by year. Number of cows sighted in a year as a proportion of available cows for that year.

Year	No. of cows available	No. of cows sighted	Sighting rate
1980	17	9	0.53
1981	20	10	0.50
1982	28	15	0.54
1983	34	13	0.38
1984	39	22	0.56
1985	41	21	0.51
1986	47	21	0.45
1987	51	18	0.35
1988	53	23	0.43
1989	52	28	0.54
1990	54	27	0.50
1991	54	26	0.48
1992	55	23	0.42
1993	57	18	0.32
1994	60	31	0.52
1995	60	32	0.53
1996	70	44	0.63
1997	75	50	0.71
1998	70	40	0.57

Table 4

Intervals between sightings for females in the 1980s and 1990s.

Category	Period	*n*	Mean (yrs)	SD
Juvenile females	1980-1989	161	1.37	0.56
	1990-1998	129	1.40	0.65
Adult females	1980-1989	118	1.93	0.84
	1990-1998	253	1.93	0.97

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 calvings 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 calvings, 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.

Table 5

Prior sighting histories for cows with six and seven year calving intervals. Calves could have been missed if cows were not observed in years 3 and 4 of a seven-year interval, or year 3 of a six year interval.

Whale ID	Year	Interval (years)	Missed years prior to calving (by year)						Missed calves possible	Southeast calving?
1004	1987	7	0						No	Y
1242	1988	6	1	2	3		5		Yes	N
1142	1990	6		2	3		5		Yes	Y
1145	1991	7	1	2		4		6	Yes	Y
1204	1991	6	1						No	Y
1240	1991	6	1	2					No	Y
1612	1992	6	1	2	3		5		Yes	Y
1241	1995	6	0						No	Y
1114	1996	6	0						No	Y
1142	1996	6	1	2			5		No	Y
1281	1996	7	1						No	Y
1014	1997	6	1	2	3				Yes	Y
1118	1997	7	1	2	3				Yes	Y
1240	1997	6	1						No	Y
1243	1997	6	1	2					No	Y
1248	1997	7	1	2	3	4	5	6	Yes	N
1310	1997	7	1		3	4	5		Yes	Y
1233	1998	6	1	2	3	4	5		Yes	Y
1315	1998	6	1	2	3	4			Yes	Y
1321	1998	7	1	2	3	4	5		Yes	Y
1515	1998	6	1	2	3	4	5		Yes	Y

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 CFMY 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 in assimilating 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).

ACKNOWLEDGEMENTS

We thank Phil Clapham, Peter Best, and an anonymous reviewer, whose comments greatly improved the manuscript. The data presented here were collected by members of the North Atlantic Right Whale Consortium – particular thanks are due the staff of the Center for Coastal Studies, the New England Aquarium, the University of Rhode Island, Woods Hole Oceanographic Institution, the Georgia Dept. of Natural Resources, and the Florida Marine Research Institute. Supporters of this work include the US National Marine Fisheries Service, the Island Foundation, the International Fund for Animal Welfare, the Oak Foundation, the Irving Oil Company, the Davis Foundation, the Office of Naval Research, the Canadian Dept. of Fisheries and Oceans, World Wildlife Fund and the Massachusetts Environmental Trust.

REFERENCES

Barlow, J. 1990. A birth-interval model for estimating cetacean reproductive rates from resighting data. *Rep. int. Whal. Commn* (special issue) 12:155-60.

Best, P.B. 1990. Natural markings and their use in determining calving intervals in right whales off South Africa. *S. Afr. J. Zool.* 25(2):114-23.

Best, P.B. and Underhill, L.G. 1990. Estimating population size in southern right whales (*Eubalaena australis*) using naturally marked animals. *Rep. int. Whal. Commn* (special issue) 12:183-9.

Best, P.B., Brandão, A. and Butterworth, D. 2001. Demographic parameters of southern right whales off South Africa. *J. Cetacean Res. Manage.* (special issue) 2:161-169.

Brown, M.W., Kraus, S.D., Gaskin, D.E. and White, B.N. 1994. Sexual composition and analysis of reproductive females in the North Atlantic right whale, *Eubalaena glacialis*, population. *Mar. Mammal Sci.* 10(3):252-65.

Brownell, R.L., Best, P.B. and Prescott, J.H. (eds.). 1986. *Report of the International Whaling Commission (Special Issue 10). Right Whales: Past and Present Status*. International Whaling Commission, Cambridge, UK. vi+289pp.

Caswell, H., Fujiwara, M. and Brault, S. 1999. Declining survival probability threatens the North Atlantic right whale. *Proc. Natl Acad. Sci. USA* 96(6):3,308-13.

Cooke, J.G., Rowntree, V. and Payne, R. 2001. Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Peninsula Valdés, Argentina. *J. Cetacean Res. Manage.* (special issue) 2:125-132.

Fairfield, C.P. 1990. Comparison of abundance estimation techniques for the western North Atlantic right whale (*Eubalaena glacialis*). *Rep. int. Whal. Commn* (special issue) 12:119-26.

Hamilton, P.K. and Martin, S.M. 1999. *A Catalog of Identified Right Whales from the Western North Atlantic: 1935-1997*. New England Aquarium, Boston.

Hamilton, P.K. and Mayo, C.A. 1990. Population characteristics of right whales (*Eubalaena glacialis*) observed in Cape Cod and Massachusetts Bays, 1978-1986. *Rep. int. Whal. Commn* (special issue) 12:203-8.

Hamilton, P.K., Marx, M.K. and Kraus, S.D. 1995. Weaning in North Atlantic right whales. *Mar. Mammal Sci.* 11(3):386-90.

Hamilton, P.K., Knowlton, A.R., Marx, M.K. and Kraus, S.D. 1998. Age structure and longevity in North Atlantic right whales (*Eubalaena glacialis*). *Mar. Ecol. Prog. Ser.* 171:285-92.

International Whaling Commission. 2001. Report of the Workshop on Status and Trends of Western North Atlantic Right Whales. *J. Cetacean Res. Manage.* (special issue) 2:61-87.

Kenney, R.D. 1994. Anomalous 1992 Spring and Summer distributions of right whales (*Eubalaena glacialis*) and other cetaceans in continental shelf waters off the northeastern United States and adjacent Canada. Final Report to US Marine Mammal Commission, Washington, DC, Contract No. T94070648. 65pp.

Kenney, R.D. and Kraus, S. 1993. Right whale mortality - a correction and update. *Mar. Mammal Sci.* 9(4):445-6.

Knowlton, A.R., Kraus, S.D. and Kenney, R.D. 1994. Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Can. J. Zool.* 72(7):1,297-305.

Kraus, S.D. 1990. Rates and potential causes of mortality in North Atlantic right whales (*Eubalaena glacialis*). *Mar. Mammal Sci.* 6(4):278-91.

Kraus, S.D., Moore, K.E., Price, C.A., Crone, M.J., Watkins, W.A., Winn, H.E. and Prescott, J.H. 1986a. The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). *Rep. int. Whal. Commn* (special issue) 10:145-51.

Kraus, S.D., Prescott, J.H., Knowlton, A.R. and Stone, G.S. 1986b. Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic. *Rep. int. Whal. Commn* (special issue) 10:139-44.

National Marine Fisheries Service (NMFS). 2000. Report of the Workshop on the Causes of Reproductive Failure in North Atlantic Right Whales: New avenues of research. Paper SC/52/OS14 presented to the IWC Scientific Committee, June 2000, Adelaide, Australia. [Paper available from the Office of this Journal].

Patenaude, N.J. and Baker, C.S. 2001. Population status and habitat use of southern right whales in the sub-Antarctic Auckland Islands of New Zealand. *J. Cetacean Res. Manage.* (special issue) 2:111-116.

Payne, R., Brazier, O., Dorsey, E.M., Perkins, J.S., Rowntree, V.J. and Titus, A. 1983. External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. pp.371-445. *In:* R. Payne (ed.) *Communication and Behavior of Whales*. AAAS Selected Symposia Series 76. Westview Press, Colorado. xii+643pp.

Payne, R., Rowntree, V., Perkins, J.S., Cooke, J.G. and Lankester, K. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. *Rep. int. Whal. Commn* (special issue) 12:271-8.

Schaeff, C.M., Kraus, S.D., Brown, M.W. and White, B.N. 1993. Assessment of the population structure of western North Atlantic right whales (*Eubalaena glacialis*) based on sighting and mtDNA data. *Can. J. Zool.* 71(2):339-45.

Sutcliffe, W.H. and Brodie, P.F. 1977. Whale distribution in Nova Scotia waters. *Tech. Rep. Environ. Can. Fish. Mar. Serv.* 722:1-83.