Vol. 171: 285–292, 1998 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published October 1

Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction

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ABSTRACT: Although there are a number of techniques for determining age in dead baleen whales, few exist for live, free-swimming animals. Photo-identification records of 374 cataloged individuals through 1996 were used to assess the age of first parturition, the age structure and the longevity of the North Atlantic right whale *Eubalaena glacialis*. Nearly the entire population is identified and the majority of the whales have extensive sighting histories dating from 1980, with some earlier sightings dating as far back as 1935. The observed mean age at first parturition for females with complete sighting histories (n = 13) is 8.7 yr and the age at which whales are considered adults, based on the mean age of first observed parturition for *all* known-age females (n = 20), is 9 yr. Juveniles and calves constitute 26 to 31 % of the population, considerably less than in other baleen whale species. One whale is at least 65 yr old, and reproductive histories of others span up to 29 yr. Although the 65 plus yr old whale is possibly reproductively senescent, her apparent lack of calving may be due to anthropogenic factors or to undocumented calvings.

KEY WORDS: Right whale · Age · Longevity · Reproductive senescence · *Eubalaena glacialis* Sexual maturity · Age structure

INTRODUCTION

There are a variety of techniques for estimating the age of mysticetes (baleen whales), but only some have been perfected and they are applicable only on carcasses; few exist for live, free-swimming animals. Information collected from carcasses suggest that many mysticete species are long-lived (Jonsgård 1969). Whaling data collected for fin (*Balaenoptera physalus*), gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*), and bowhead (*Balaena mysticetus*) whales incorporated a number of different age determination techniques. These included counting growth layers both in the ear plug from the auditory meatus (Symons 1956) and in the baleen plates (Ruud 1940, Tomlin 1945, Zeh et al. 1993), and counting the number of corpora (lutea and albicantia) in the uteri of females (Jonsgård 1969). Of these techniques, ear plugs, and to a lesser extent corpora, have proven to be most accurate and they indicate that baleen whales can live into their 70s and 80s. For live, free-swimming mysticetes, age determination techniques are currently limited to photogrammetry and photo-identification (Zeh et al. 1993). The former is useful for estimating ages of all whales based on assumptions about growth rates, but is less effective on older animals. The latter can provide actual ages for animals first identified as calves, and minimum ages for all others.

The northern right whale *Eubalaena glacialis* is among the most endangered of the large whales throughout its range, which includes both the North Atlantic and the North Pacific. In the North Atlantic, the eastern population appears to be nearly extinct, following prolonged and extensive whaling (Aguilar 1986). The population in the western North Atlantic is estimated to number approximately 295 individuals and occupies a range that is largely confined to the waters from Florida to Nova Scotia (Knowlton et al. 1994). Much has been learned about this population over the last 16 yr of extensive study using photo-

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identification. Previous analyses have indicated that females calve every 3 to 5 yr, are primiparous on average at 7.5 yr, and the population is growing at 2.5% yr^{-1} (SE = 0.3%), which is only a third the rate of 2 populations of southern right whales (*E. australis*) (Best & Underhill 1990, Payne et al. 1990, Knowlton et al. 1994). However, to date, there has been no evaluation of the age structure of the population. The problem of aging right whales has been compounded by the fact that the ear plugs in this species have proven to be unreadable (Omura et al. 1969). Furthermore, the few carcasses that have been retrieved have decomposed internally so quickly that the corpora were undetectable.

Here we assess the age structure of the western North Atlantic right whale population using photo-identification. We provide new data on the age of first parturition, the age of sexual maturity, and longevity. The sighting and reproductive histories of 7 whales with known minimum ages greater than 20 yr are presented, and the implications of this longevity on the species' reproductive span, and the possibility of reproductive senescence, are discussed.

METHODS

Identification. Right whales were individually identified by photographs of the pattern of cornified tissue (the 'callosity') on their rostra. These callosity patterns, along with body scarring and unique lip crenations, have proven reliable for long-term identification of individuals (Payne et al. 1983, Kraus et al. 1986). All identifications were confirmed by at least 2 experienced researchers.

Photographs collected by the North Atlantic right whale consortium (an informal collaboration among: New England Aquarium, Center for Coastal Studies, University of Rhode Island, Woods Hole Oceanographic Institution, and Marineland of Florida), together with a number of other sources, over the period 1935 through 1996 have been compiled, analyzed and integrated into a catalog maintained at the New England Aquarium. Consistent effort dedicated to photo-identification began in 1980, and photographs were collected from the entire known migratory range. This includes the only known calving ground along the southeastern coast of the United States (Kraus et al. 1986), and the feeding grounds off the northeastern U.S., Canada (Winn et al. 1986), and as far north as Greenland (Knowlton et al. 1992).

Each individual in the catalog was assigned a 4-digit catalog number. Because the callosity pattern is not well established until the latter half of their first year, calves were assigned catalog numbers only if they were well photographed on the feeding grounds while still associated with their mothers. Therefore, some calves that were photographed solely on the calving ground were not photo-identified and could not be added to the photo-catalog (Hamilton et al. 1995). The existing catalog of identified whales numbers 374 individuals photographed through 1996. We believe that the majority of the population has been identified, due to the small number of new, non-calf individuals sighted each year (1 to 6 yr^{-1} in the 1990s; authors' unpubl. data). The actual population is likely less than the number in the catalog once the number of known and presumed mortalities are considered. Although complete catalog data were fully analyzed only through 1996, 8 calving records from January 1997 are included as they add substantially to information on reproductive span and age at first parturition.

Age at first parturition. In order to most accurately assess the age structure of the population, an analysis of the age of first parturition was conducted to test an earlier assumption that whales are adult at age 10 (yr) (Knowlton et al. 1994). Sighting histories for all females of known age that were 5 yr or older and were presumed to be alive in 1996 were analyzed (n = 41). Whales were classified as known-age if they were observed and well photographed in their year of birth. Five years of age was used as the lower boundary as it is the earliest known age at first parturition for any right whale (Payne et al. 1990, Knowlton et al. 1994, P. B. Best pers. comm.). To investigate the possibility that the first calving for some whales had been missed due to a gap in their sightings, we reviewed the sighting histories for the 41 known-age females. For calving females, a missed sighting year was only counted as a possible missed calving year if it was 3 yr or more prior to a year of known calving (see review of calving intervals in Knowlton et al. 1994) and the whale was 5 yr or older in that missed sighting year. For whales that had never been seen with a calf, a minimum age of 5 was the only criterion for their inclusion in the analysis.

Once this analysis was completed, we looked at the percentage of whales that had definitely not calved for each age. A whale was determined not to have calved only for those years prior to either its first known calving or its first possible missed calving. For example, if a non-parous whale was sighted every year for 15 yr except its 7th year, it was considered as definitely not calving at ages 5 and 6, but was *not* considered as definitely non-parous for any of the years after age 6 because it could have had a calf at age 7. Similarly, if a non-parous whale was not sighted in its 5th year, it was never counted as a definite non-parous whale. This analysis does not account for miscarriages or early calf mortality. It assumes that a whale did not have a calf if it was sighted without a calf.

Age structure. In order to assess the current age structure of the population, each whale in the catalog was categorized as adult, juvenile, or unknown as of 1996, the last year for which fully analyzed data were available. Juveniles were defined as individuals of known age who were less than 9 yr old in 1996 (Payne et al. 1990, this paper), including calves. Calves were considered calves for the calendar year of their birth (because peak calving for this population is in late December/early January; Kraus et al. 1993). Adults were defined in 1 of 3 ways: (1) whales of known age who were at least 9 yr old in 1996, (2) whales of unknown age whose sighting histories spanned 8 yr or more (because they were at least 1 yr old when first sighted), and (3) any parturient female, irrespective of the length of her sighting history. With the exception of these latter females, whales of unknown age and with sighting histories spanning less than 8 yr were categorized as of unknown-age class.

To determine the age structure of the living population, it was first necessary to identify all deceased whales and eliminate them from our tabulations. Some deceased whales float or are towed to shore and can be identified from the cataloged population. However, the data suggest that many other mortalities remain undocumented at sea (Kraus 1990). In an attempt to estimate the number of whales that have died, but whose deaths were not documented, we applied Knowlton et al.'s (1994) criteria for presuming mortalities based on sighting histories. Whales that were not sighted for more than 5 yr were presumed dead and were eliminated from our sample at the end of the 6th year. Although this time span is somewhat arbitrary, the sightings data of identified individual right whales indicate that it is rare for a living whale to go unphotographed for more than 6 yr. Of the 374 whales in the catalog, only 9 individuals, or 2.4% of the known population, have been resighted after longer gaps. However, lack of sightings of an individual can be caused not only by a death, but also by a reduction in photographic effort. For example, there was an apparent increase in presumed dead whales from 1994 to 1996, but this increase may have occurred because survey effort in the 2 primary offshore habitats, Great South Channel and Browns Bank, was severely curtailed after 1989 (Hain et al. unpubl.). In order to account for this possible bias, we also examined the age structure of the population assuming that all presumed dead whales were alive.

There is similar uncertainty in the actual status of whales in the unknown-age-class category. We decided that a range of possible ages for these individuals would be most informative. Therefore, we looked at the population treating the unknown-age-class whales in 3 different ways: (1) eliminating them from the analysis all together, (2) considering them all to be adults, and (3) considering them all to be juveniles.

RESULTS

Age at first parturition

There were 45 records of known-age females that were 5 yr or older. Four were females that were presumed to be dead and were removed from the analysis. Of the remaining 41, 20 had given birth and 21 had never been seen with a calf. The observed ages of the 20 primiparous whales ranged from 5 to 14 (Fig. 1). The mean age at first parturition was 9.6 yr (SD 2.33), the median was 9.5 and the mode was 10. However, 7 of the 20 primiparous females each had at least 1 year when an earlier calving could have been missed. If these 7 whales are removed from the analysis, the calvings at ages 11, 12 and 14 would be removed and the numbers in the 9, 10 and 13 yr age-class categories would drop to 3, 4, and 1 respectively (Fig. 1). The mean would be reduced to 8.7 yr (SD 2.10) and the median changed to 9 yr, but the mode would remain at 10.

To investigate the likelihood of these and other missed calvings having occurred, the sighting histories of all of the 41 living females were analyzed to assess the percentage of whales that definitely *did not* calve at or before a given age (Fig. 1). Of all whales that had reached the age of 5 (n = 41) 78% had definitely not calved by that age. The percentages for the other age classes were: 64% of those that had reached the age of 6 (n = 36), 55% of those that had reached the age of 7 (n = 33), 46% of those that had reached the age of 8 (n = 28), 27% of those that had reached the age of 9 (n = 26), 11% of those that had reached the age of 10 (n = 19), <1% for those that had reached the ages of 11 and 12 (n = 15 and 14 respectively), and none for ages greater than 12. There were 2 whales older than 12 that had not been observed with a calf, but both had sighting gaps when a calving could have been missed.

Age structure with presumed mortalities

Of the 374 whales in the catalog in 1996, nine whales were documented as dead (i.e. photographed dead on the beach and identified to the catalog) and 82 were presumed to be dead. Of the remaining 283 whales thought to be alive in 1996, 122 whales were of known age: 70 were juveniles and 52 were adults. An additional 143 whales were determined to be adults due either to a 9+ yr sighting history or a known calving,

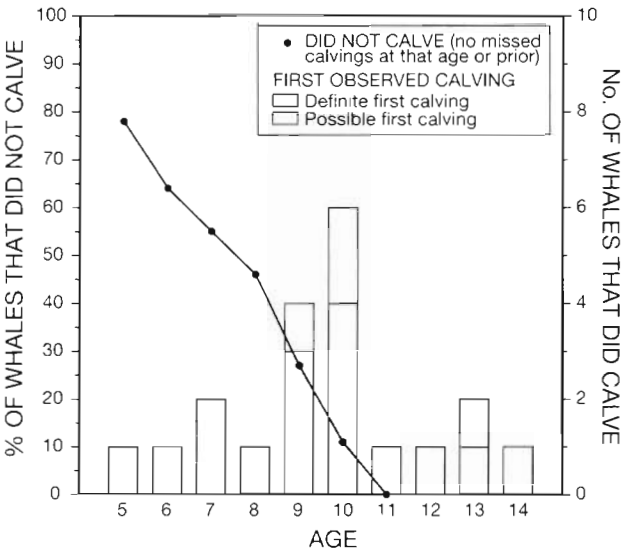

Fig. 1. *Eubalaena glacialis*. Assessment of the age of first observed parturition for 41 known-age female right whales. Circles represents the percentage of whales that had reached each age and definitely not calved by that age. Shaded bars show the age of parturition for the 13 whales whose first calving is definite (i.e. there were no possible prior missed calvings). Empty bars represent the age of the remaining 7 parturient whales that may have had a prior missed calving

thus increasing the number of adults to 195. The age class of the remaining 18 whales was considered unknown (Table 1).

If these 18 whales were eliminated from the analysis, the 70 juveniles would represent 26.4% of the living population (n = 265). If these 18 whales were included and all considered to be adults, the known juveniles would make up 24.7% of the population (n = 283). However, the data suggest that the majority of these unknowns are probably juveniles which were not identified in their calf year. Between 1980 and 1995, there were 29 calves born that were not photo-identified in their first year, and there have undoubtedly been other undocumented calves (Hamilton et al. 1995). If we consider all of the unknowns to be juveniles, then juveniles would constitute 31.1% of the living population. Thus, the range of juvenile percentages if presumed dead whales are treated as dead is 24.7 to 31.1%, with the data favoring the higher end of the range (Table 2).

Table 1. *Eubalaena glacialis*. Age structure of the cataloged population of 374 right whales, 1935–1996, with 82 whales presumed dead. Adults are either of known age (9 yr or greater), are assumed to be adults based on a sighting history of 8 yr or greater, or have given birth. Juveniles/calves are whales of known age 0–8. Unknown-age individuals are whales whose year of birth is unknown and whose sighting history is less than 8 yr

Age category	Male	Female	Unknown sex	Total
Adult				
Known age	25	26	1	52
Assumed age	64	58	21	143
	89	**84**	**22**	**195**
Juvenile/calf				
Known age	**25**	**23**	**22**	**70**
Unknown age	**4**	**9**	**5**	**18**
Dead				
Known	5	4	0	9
Presumed				
Known age	7	4	10	21
Unknown age	12	20	29	61
	24	**28**	**39**	**91**
Total	**142**	**144**	**88**	**374**

Age structure without presumed mortalities

If the whales that were presumed to be dead were all considered alive, the living population in 1996 would be 365 whales. The 82 whales that had been presumed dead fell into the follow categories: 75 adults (15 known age, 60 assumed), 6 juveniles (all known age) and one unknown age class. This increased the pool of known-age whales by 21, making a total of 143: 76 juveniles and 67 adults. An additional 203 (60 of which had been presumed dead) were determined to be adults due either to an 8 yr or greater sighting history or a known calving, thus increasing the number of adults to 270. The age class of the remaining 19 (one of which had been presumed dead) whales was considered unknown (Table 3).

If these 19 unknown-age whales were eliminated from the analysis, the 76 juveniles would represent 22.0% of the living population (n = 346). If these 19

Table 2. *Eubalaena glacialis*. Comparison of the age structure of the living population when whales are presumed dead and if all presumed dead whales were actually alive

	Adults	Juveniles
With presumed mortalities		
If all individuals of unknown-age class are eliminated	73.6% (n = 195)	26.4% (n = 70)
If all individuals of unknown-age class are considered adults	75.3% (n = 213)	24.7% (n = 70)
If all individuals of unknown-age class are considered juveniles	68.9% (n = 195)	31.1% (n = 88)
With no presumed mortalities		
If all individuals of unknown-age class are eliminated	78.0% (n = 270)	22.0% (n = 76)
If all individuals of unknown-age class are considered adults	79.2% (n = 289)	20.8% (n = 76)
If all individuals of unknown-age class are considered juveniles	74.0% (n = 270)	26.0% (n = 95)

Table 3. *Eubalaena glacialis*. Age structure of the cataloged population of 374 right whales, 1935–1996, if all whales that are presumed dead were alive in 1996. Adults are either of known age (9 yr or greater), are assumed to be adults based on a sighting history of 8 yr or greater, or have given birth. Juveniles/calves are whales of known age 0–8. Unknown-age individuals are whales whose year of birth is unknown and whose sighting history is less than 8 yr

Age category	Male	Female	Unknown sex	Total
Adult				
Known age	31	28	8	67
Assumed age	76	78	49	203
	107	**106**	**57**	**270**
Juvenile/calf				
Known age	**26**	**25**	**25**	**76**
Unknown age	**4**	**9**	**6**	**19**
Dead				
Known	**5**	**4**	**0**	**9**
Total	**142**	**144**	**88**	**374**

whales were included and all considered to be adults, the known juveniles would make up 20.8% of the population (n = 365). As suggested above, the more likely scenario is that many of the whales of unknown-age class are juveniles, in which case juveniles would constitute 26.0% of the living population. The range of juvenile percentages if presumed dead whales are treated as alive is 20.8 to 26.0%, with the data favoring the higher end of the range (Table 2).

Longevity and reproductive histories

Of the 374 cataloged individuals, 7 have been sighted over a period greater than 20 yr (Table 4). Whales no. 1045, 1047, 1135, 1127, 1240, 1004 and 1619 have sighting histories spanning 60, 31, 29, 28, 23, 22 and 22 yr respectively. All but no. 1047 were seen with a calf at least once.

Whale no. 1045 was first photographed in 1935 off the Florida coast when her calf was killed by fishermen (Levick 1935). She and her calf were shot repeatedly with rifles and the calf was harpooned. The mother remained with her calf throughout the 6 h battle and abandoned it only after it died. Fortuitously, Edwin (John) Levick, a professional photographer, was on board to document the event. Although his negatives and prints have since been lost, the resulting magazine photograph was clear enough to be matched to more recent photographs of this whale (Fig. 2). She was last sighted in 1995 near George's Bank with a large propeller gash on the right side of her head. Her only documented calving was in 1935. Since the youngest known age at first parturition for a female right whale is 5 yr (Knowlton et al. 1994), the most conservative estimate of no. 1045's minimum age in 1995 is 65. Given that the average age at first birth is 9 yr (Payne et al. 1990, this paper), a more likely minimum age for no. 1045 in 1995 is 69.

When whale no. 1047 was first photographed in March 1957, the shape of the head (i.e. a high coaming and a concave rostrum) was consistent with that of a juvenile, possibly a 2-yr-old (authors' unpubl. data). If we assume that at the first sighting no. 1047 was at least 1 yr old, its minimum age when last sighted in August 1988 was 32 yr. Using the 6 yr criterion, this whale is now presumed to be dead.

Whale no. 1135 had a calf with her when first sighted in February 1967. She is known to have given birth again in 1974, 1981, 1984, 1987, and 1991 and was sighted most recently in September 1996 with her 7th documented calf. A conservative estimate of her minimum age in 1996 is therefore 34 yr, and her known reproductive history spans 29 yr.

Whale no. 1127 was first sighted, apparently as an adult, as suggested by head shape and body length, in May 1966. She gave birth in 1976, 1981, 1984, 1987, and 1990 and was last sighted in April 1994 with her

Table 4. *Eubalaena glacialis*. Listing of 7 right whales whose sighting histories span more than 20 yr. Cat no. refers to the individual's catalog number. The first age listed is the absolute minimum age; the age in parentheses is the estimated minimum age determined by the individual's status at first sighting. Reproduction span represents the number of years between the first documented calving and the most recent calving and could only be calculated for whales that had calved at least twice. Interim sighting years in bold indicate calving years. F: female; U: unknown

Cat no.	Sex	Year first sighted	Status	Interim sightings	Year last sighted	Status	Minimum age	Reproduction span (yr)
1045	F	1935	With calf	59, 80, 85, 92	1995	Adult	60 (65)	–
1047	U	1957	Juvenile?	78, 81	1988	Adult	31 (32)	–
1135	F	1967	With calf	**74**, 80, **81**, 82, **84**, 85, **87**, 90, **91**, 93, 94	1996	With calf	29 (34)	29
1127	F	1966	Adult?	74, **76**, 79, **81**, **84**, **87**, **90**	1994	With calf	28 (31)	18
1240	F	1974	With calf	79, **82**, **85**, 88, 89, 90, **91**, 93, 94, 95	1997	With calf	23 (28)	23
1004	F	1975	Unknown	**80**, 85, **87**, 89, **90**, 93, **94**, 95	1997	With calf	22 (23)	17
1619	F	1970	Unknown	86, **87**, 88, **90**	1992	Adult	22 (23)	3

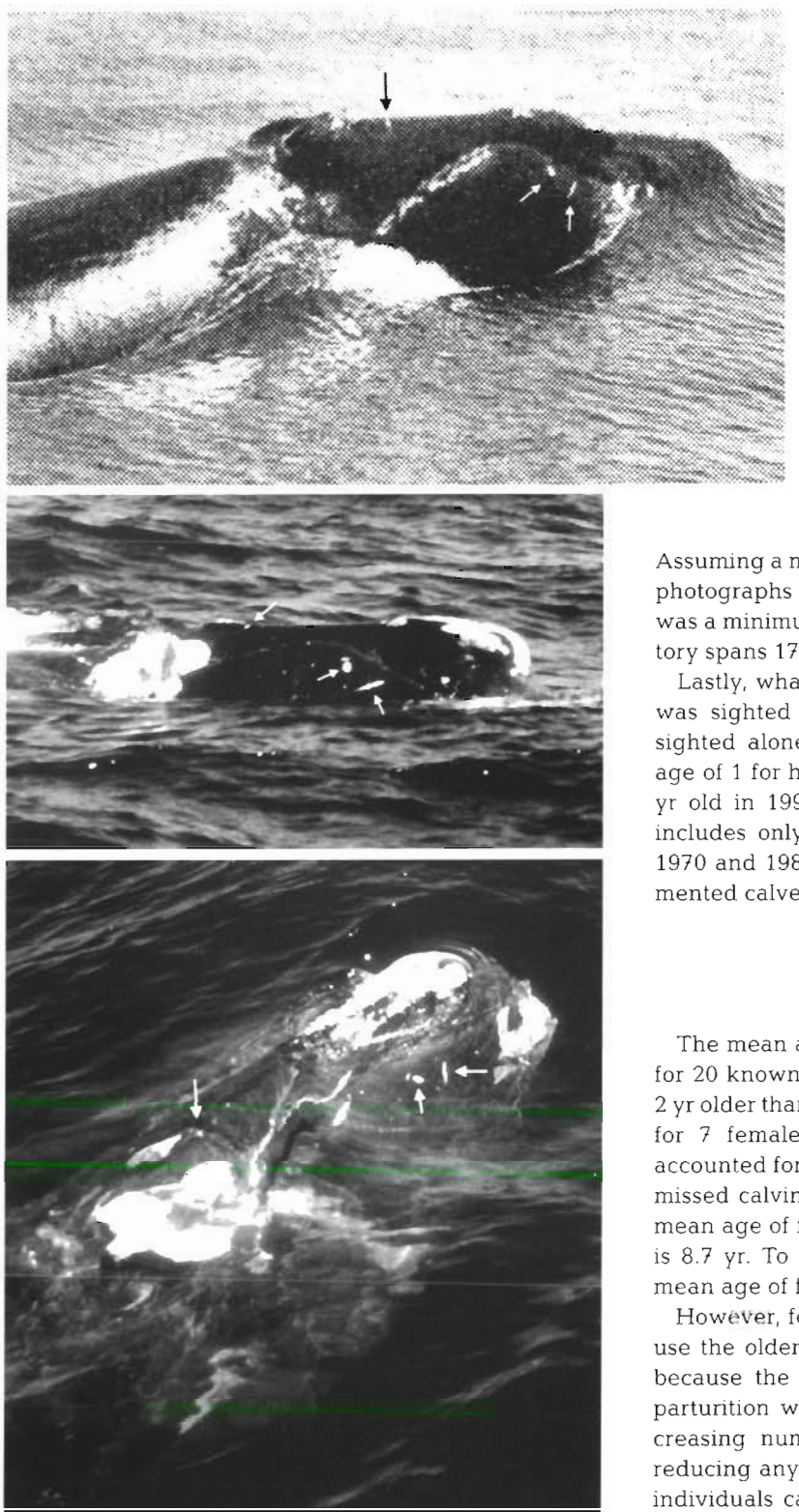

Fig. 2. Whale No. 1045 photographed on March 24, 1935, by Edwin Levick (top) and on August 13, 1995, by Brian Chmielecki (bottom photographs). Note the location and orientation of the 2 scars on the lip and 1 on the head, which were used, along with the callosity placement, to confirm the identification

6th documented calf. Conservatively assuming an age of at least 3 at her first sighting, no. 1127 was a minimum of 31 yr old at her last sighting with a sighting history spanning 28 yr. Her reproductive history spans 18 yr.

Whale no. 1240 was first sighted in 1974 with a calf near Long Island, New York. She was also sighted with a calf in 1982, 1985, and 1991 and was last sighted in 1997 with her 5th documented calf. A conservative estimate of her age in 1997 is 28 and her reproductive history spans 23 yr.

Whale no. 1004 was first sighted in 1975. She was sighted with a calf in 1980, 1987, 1990, and 1994 and was last sighted in 1997 with her 5th calf. Assuming a minimum age of 1 for the first sighting (the photographs show that she was not a calf), no. 1004 was a minimum of 23 in 1997 and her reproductive history spans 17 yr.

Lastly, whale no. 1619 was first sighted in 1970. She was sighted with a calf in 1987 and 1990 and last sighted alone in 1992. Again, assuming a minimum age of 1 for her first sighting, she would be at least 23 yr old in 1992. Although her known calving history includes only 3 years, she was not sighted between 1970 and 1986 and may well have had some undocumented calves during that period.

DISCUSSION

The mean age of 9.6 yr for first observed parturition for 20 known-age females reported here is more than 2 yr older than Knowlton et al.'s (1994) findings of 7.5 yr for 7 females. However, neither of these analyses accounted for possible missed calvings. When possible missed calvings are eliminated from our analysis, the mean age of first calving for the remaining 13 females is 8.7 yr. To be conservative, we adopt 8.7 yr as the mean age of first observed calving.

However, for the age structure analysis, we opted to use the older age to classify adult whales. We did so because the evidence suggests that the age of first parturition will continue to increase over time as increasing numbers of older whales give birth, thus reducing any sampling bias introduced by precocious individuals calving early. The population of southern right whales off Argentina showed a similar increase in age at first parturition as the time span of that data set increased (Payne 1986, Payne et al. 1990).

There are also several indications that we are not missing calvings, which would mean that the mean

age of first parturition of 9.6 yr for all 20 females would be more accurate. All 7 of the whales with possible missed calvings are regularly seen in the Bay of Fundy and all brought their known calves to the Bay. Given that many females show site fidelity to nursery areas (Schaeff et al. 1993), it is unlikely that we would have missed documenting these particular females and their calves in the Bay of Fundy as well as on the calving ground along the southeastern coast of the United States and the other feeding/nursery grounds in Massachusetts Bay, especially considering the substantial survey effort in all 3 areas. Lastly, there were 7 whales that definitely had not calved by age 9 and the median and modes of both the 20 females and the subset of 13 indicate that the age of first parturition was between 9 and 10 yr. With so many indications that the older age of first parturition is more accurate, we used the mean of 9.6 yr to determine adulthood.

If we assume that northern right whales have a similar gestation period to the 12–13 mo estimated for the southern species (Best 1994), then the higher mean of 9.6 yr for first parturition indicates that females are adults by 8.6 yr. If we round the number up, the age of sexual maturity would be 9 yr. This reduces the age at which a right whale is considered an adult by 1 yr from the 10 yr reported by Knowlton et al. (1994), who used uncorrected data from right whales off Argentina (Payne et al. 1990). It also effectively reduces the percentage of juveniles in the population.

If, as the data suggest, 26 to 31% of the population are juveniles, then the pool of juveniles for this species is considerably less than for other mysticetes. Zeh et al. (1993) estimated the percentage of juveniles (including calves) in the population of Bering Sea bowheads to be 56 to 58%. Rice & Wolman (1971) estimated that 61% of the 168 gray whales analyzed were immature. They suggested that the proportion of immature whales in populations should be large while the population is growing and should decrease once the population begins to stabilize. It is implausible that this population would reach carrying capacity and stabilize at a mere 300 to 350 individuals. It is more likely that other factors limiting reproductive rates are keeping the percentage of juveniles abnormally low. Knowlton et al. (1994) suggested that these factors might include effects from inbreeding, competition for food resources and sublethal effects of toxic contaminants. Since that paper, the mean calving interval for all females has continued to increase (New England Aquarium unpubl. data) and the potential effects of both food limitation and contaminant burdens are being actively investigated. It is also possible that, if some of the reproductive females are quite old, the reduced reproduction is being caused in part by a decrease in pregnancy success such as has been documented in other mammals as they near death (Packer et al. 1998).

A 60 yr match is the longest documented match for any whale and may well be the longest documented sighting history for a free-ranging mammal. An absolute minimum age of 65 for a right whale, although previously undocumented, is certainly not unexpected. Rice & Wolman (1971) estimated gray whales to have a maximum age of 77 using the corpora count and 67 using ear plug laminae. Using ear plugs, Mizroch (1981) showed fin whales living to ages of 76 with pregnant females caught at ages ranging from 60 to 76. Aguilar & Lockyer (1987) showed male fin whales living into their 80s and George et al. (1995) provided evidence of bowheads living up to 100 yr.

With a number of factors impeding right whale recovery (i.e. entanglements and ship strikes, and possibly inbreeding and habitat degradation), a long life span may be one of the few hopes for the species' recovery. If there is no reproductive senescence, the longer the whales live, annual recruitment should grow as older females continue giving birth to at least some female calves. Although whale no. 1045's apparent lack of calving since 1935 suggests that she may be reproductively senescent, this is unlikely. To date, the only whale species that have been documented to exhibit reproductive senescence are killer whales and pilot whales (Marsh & Kasuya 1986, Olesiuk et al. 1990). It is more likely that we have either missed calvings due to her sporadic sighting history or that her lack of calving is the result of anthropogenic factors such as contaminants (Subramanian et al. 1987) or even the gunshot wounds sustained in 1935.

It is clear that photo-identification is at present the most effective means of determining minimum ages for live right whales. Although we currently have only 7 matches spanning a substantial period of time (more than 20 yr), this is not an indication of an inherent weakness in the technique. Over the next 20 to 30 yr we can expect both the span of sightings as well as the number of whales with substantial sighting histories to increase. With the majority of the population identified, we are in a unique position to use this age determination technique to gain new insight into the population dynamics and life history of the species. The effectiveness of this tool will continue to increase if this long-term effort can be maintained.

Acknowledgements. It is only through the collaboration of the right whale consortium members and many others that this information is available. Special acknowledgements go to Drs William Watkins, William Schevill, Howard Winn, Robert Kenney, and Charles 'Stormy' Mayo, and to Melba and David Caldwell, who were instrumental in the formation of the right whale consortium. The 1995 match to whale No. 1045 was only possible with the help of Fred Wenzel, Randall Reeves, David

Williams of the DCW & Associates detective agency, and Brian Chmielecki. Carolyn Miller, Cathy Quinn, Debie Meck and the Woods Hole Oceanographic Institution helped with the reproduction of No. 1045's images. There is a long list of people who have helped maintain the catalog over the years making this data available, but special thanks go to Martie Crone for her years of dedicated work over the light table and in the field. Support was provided by the National Marine Fisheries Service, Island Foundation, Davis Conservation Foundation, World Wildlife Fund–U.S., Marine Mammal Commission, Minerals Management Service, and faithful sponsors of the New England Aquarium's Right Whale Sponsorship Program.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: January 7, 1998; Accepted: June 8, 1998
Proofs received from author(s): August 31, 1998