Errors in age estimates of North Atlantic minke whales when counting growth zones in *bulla tympanica*

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ABSTRACT

Age estimation of common minke whales (*Balaenoptera acutorostrata*) has always been difficult, and the accuracy of the current method of counting growth layer groups (GLGs) in the periosteal zone of the *tympanic bulla* has been questioned. To evaluate this method, two readers aged three sections from each of right and left *bulla tympanica* from 35 male and 57 female North Atlantic minke whales. A single age estimate with variance was calculated for each whale using General Linear Mixed Model Poisson based regression, and this estimate was compared with the number of ovulations and body length to evaluate the bias of the age determination method. The results showed a poor fit between age and number of ovulations with $R^2 = 0.0014$. Bias was estimated to be a 37% underestimate of 'true' age assuming an ovulation rate of one per year and age at sexual maturity of eight years. Precision of the bulla age estimates was lower than those of Antarctic minke whales aged using the earplug method. The high bias reduces the applicability of the bulla method in routine age-determination with a management objective. Other age determination methods for the species should be improved or developed to ensure proper monitoring of demography and life history for the North Atlantic minke whale.

KEYWORDS: COMMON MINKE WHALE; ATLANTIC OCEAN; AGE DETERMINATION; AGE AT SEXUAL MATURITY

INTRODUCTION

Precise, unbiased age estimates are important requirements in managing different stocks of terrestrial and aquatic organisms (Morris, 1972; Birney *et al.*, 1975). Age is especially important when one wishes to study the age structure, life-history and catch-at-age history of the population in question (Nuckle and Bergeron, 1983). Determining the correct age of an individual is often difficult and errors can lead to an incorrectly assigned age (Bowering and Nedraas, 2001; Richards *et al.*, 1992; Olsen and Skaug, 2002). The difference between the true age *a* and the estimated age *A* is a measure of the bias of the age estimate, while the variance of several independent age estimates of the same individual is a measure of the precision of the estimate. Poor precision and high bias can each lead to errors in the demographic parameters required for study (Schnute and Richards, 1995), and it is important that these are investigated and quantified. The North Atlantic common minke whale stock is currently exploited by Norwegian whalers and Greenland Inuit hunters (IWC, 1999), and estimating correct age has been a problem for a long time. In the Norwegian minke whale studies, less than 20% of the animals could be aged using ear plugs (Christensen, 1992) mainly because of difficulties with plug removal and collection. Instead, whales from the Norwegian catch have been aged by counting the annual growth layer groups (GLGs) in the periosteal layer of the ear bone, *bulla tympanica* (Christensen, 1981). Two early follow-up analyses indicated that there was an error in ageing when using the bulla method (Larsen and Kapel, 1983; Sukhovskaya *et al.*, 1985), but the error was not quantified until Christensen (1995) found an 80% agreement (± 1 year) between three readers. However, a later study by Olsen (1997) indicated that the bulla method underestimated the 'true' age. These disagreements necessitated the study of errors in age estimates based on the bulla method with the aim of quantifying both precision and bias of the method. A project was started in 1999 with three aims: (1) evaluate the bias of the method through a multi-reader experiment; (2) estimate the precision of bulla ageing method through a multi-reader experiment; (3) evaluate the reliability of the bulla method when used in routine age estimation. The focus of the present study is on bias (1) and use of the bulla method in routine age estimation (3). The question of precision (2) has been dealt with in detail in Olsen and Skaug (2002).

Bias

The bias of a single age estimate is the difference between estimated age *A* and true age *a*, and the ideal method of studying this is by conducting a study on known-age animals. For practical reasons this is impossible for minke whales, and one is left with two alternatives: (1) to compare bulla age estimates with other independent estimates of age (i.e. age estimates based on alternative methods); or (2) to compare bulla age estimates with independent growth parameters. No validated alternative ageing method currently exists for North Atlantic minke whales, which leaves comparing bulla age with different measures of relative age i.e. number of ovarian scars (ovulations) and length.

Fin whales (*Balaenoptera physalus*) and Antarctic minke whales (*Balaenoptera bonaerensis*) have been shown to have a regular ovulation rate throughout life (Laws, 158; Ohsumi and Masaki, 1975), and from studies of pregnancy rates (Christensen, 1975; Olsen, 1997) North Atlantic minke whales seem to share this characteristic. After ovulation, the ruptured follicle increases in size and becomes a *corpus luteum*, which lasts through pregnancy and lactation, after which it shrinks to a smaller size (minimum size is less than 1cm in North Atlantic minke whales) and is called a *corpus albicans* which persists for life (Laws, 1958). Thus, the ovaries of sexually mature minke whales have a permanent record of the ovulation history of the individual. Comparing the true age of minke whales with the number of ovulations (found by counting *corpus lutea* and *alibicans* in the ovaries) would yield a plot fitting within the area delimited by the error bars in Fig. 1. The error bars delimit the range of number of ovulations for a whale at a given age based on the ovulation rate. The upper limit is based on an ovulation rate of two ovulations per year, while the lower is based on a biennial ovulation rate, which are realistic upper and lower limits for the species. The 'X's plotted in the middle are based on an annual ovulation rate, which is the best current estimate for North Atlantic minke whales based on the high (80-98%) annual pregnancy rates of mature females (Jonsgård, 1951; Christensen, 1975; Olsen, 1997). However, a higher ovulation rate is not unlikely considering that in general, mammals can have spontaneous abortions in early pregnancy and new ovulation usually follows (Laws, 1958).

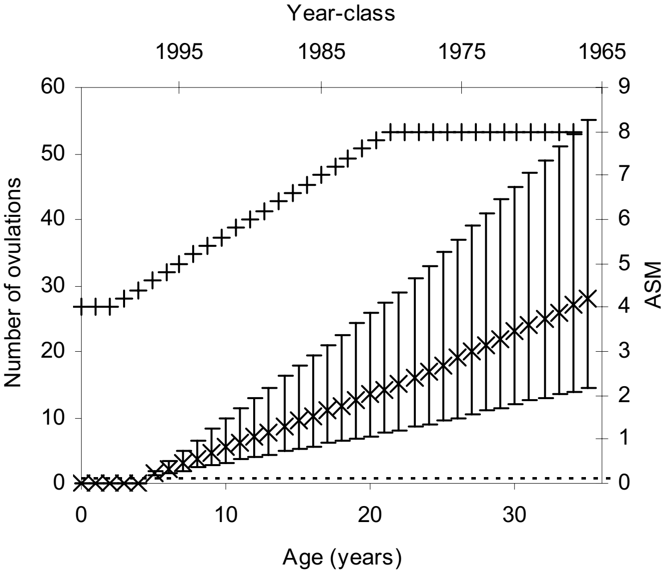

Fig. 1. Theoretical increase in the numbers of ovulations with age of female minke whales given an annual ovulation rate, and a reduction in age at sexual maturity (ASM) from eight years for the 1980 year-class to four years for the 2000 year-class. The error bars represent limits given an ovulation rate of 2*year^{-1} (upper bar) and 0.5*year^{-1} (lower bar). The first ovulation is indicated by the hatched horizontal line. X = ovulations; + = ASM.

To model a possible density-dependent decline in age at attainment of sexual maturity (ASM) the number of ovulations plotted in Fig. 1 are corrected for a decrease in ASM from eight years in 1980 to four years in 2000, where knife-edge maturation for all year-classes is assumed. The upper and lower limits of ASM were chosen deliberately and deemed realistic as ASM was estimated to eight years (±0.7 years, 95% confidence interval) by Olsen (1997), and recently to 5.8 years (±3 years, 95% confidence interval) by Olsen and Sunde (2002). Fig. 1 shows that regardless of variable ovulation rate or a decline in ASM an increase in ovulations with age could be expected if the age estimates were accurate (unbiased).

Body length increases with age, and can be a useful indicator of relative age when monitoring young year-classes as these can be identified and annual growth measured. However, mammals do not grow forever, and generally reach a maximum body size soon after attainment of sexual maturity (e.g. Brody, 1945). The sexes also have different growth patterns and different maximum body lengths. In this case female minke whales grow markedly larger than the males. In addition, there are large individual differences in physical growth. Physical growth can be modelled by using one of several non-linear growth equations. One of these is the von Bertalanffy equation (Equation 1), which was used with success by George *et al.* (1999) and Olsen and Sunde (2002) to model body length versus age estimated using the aspartic acid racemisation technique (Olsen and Sunde, 2002). To facilitate comparison with these and other studies, this growth model was used in the analysis.

Von Bertalanffy growth equation:

$$Length = L_{MAX} - L_{MAX} \times e^{(k \times t_0 - k \times age)} \qquad (1)$$

L_{MAX} is the maximum body length, k is the growth rate, and t_0 is the age at length 0.

Fig. 2 plots minke whale body length with age based on published estimates of length at birth (280cm, as presented by Jonsgård (1951)) and sex-specific maximum body length (male = 812, female = 840), calculated from the 20% largest males and females in the data (518 male and 1,264 female) used by Olsen (1997).

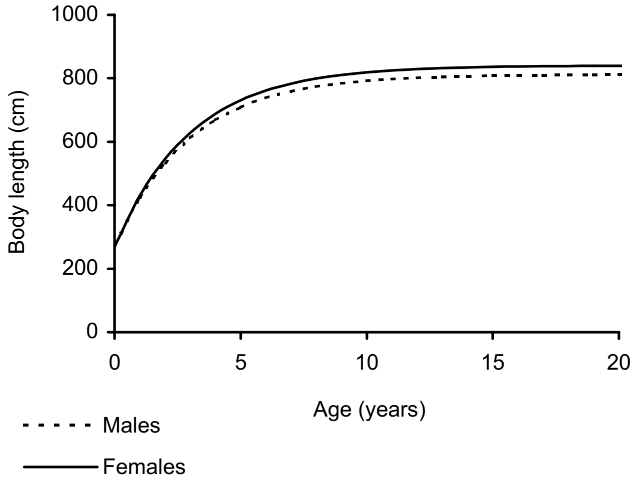

Fig. 2. Physical growth of male and female minke whales modelled by the von Bertalanffy growth equation where L_{MAX} was calculated from data in Olsen (1997). The parameter k (growth rate) was the same as estimated by (Olsen and Sunde, In press), while t_0 was chosen such that length at birth ≈ 280cm (from Jonsgård, 1951).

Precision

Precision, or random error, is a measure of how close agreement there is between parallel age estimates of the same whale. Precision is dependent on biological factors determining the formation of GLGs in bullae, and on the subjective choices made by the reader when analysing a particular bulla. It is of interest to quantify the error as a whole, and what part is caused by biological factors and what is caused by reader variability. Olsen and Skaug (2002) developed a method to estimate the variance of multiple age estimates and divided this into different components, to then make an estimate of the age of an individual. The same method is employed in the present study to estimate the age and variability based on multiple readings of bulla GLGs.

MATERIALS AND METHODS

Right and left bullae were collected from 35 male and 57 female minke whales caught onboard two Norwegian whaling vessels operating in the North Sea and Central Atlantic (ES and CA, IWC small management areas, see IWC, 1994) in May-July 1999 and 2000 (Table 1). From 28 of these, only one bulla was collected as the other was destroyed after the grenade on the harpoon detonated, or it was inaccessible during flensing. The length distribution of the sampled whales is shown in Fig. 3. At the laboratory the bullae were cleaned and 0.2mm thick transverse segments were cut from the medial part of each bulla using a dual-bladed circular saw. Three such segments were cut

Table 1

Whale number, minimum and maximum age read, number of parallel age readings from a whale (*n*), sex, number of ovulations (ov.), standard body length, estimated age (based on GLMM regression) and standard deviation of the age estimate from reading left and right *bulla* from 92 minke whales caught in the North Sea in 1999 and 2000. An * after 'whale' indicates that only one *bulla* was collected.

North Sea								
Whale	Min.	Max.	*n*	Sex	Ov.	L(cm)	Est. age	SD Est.
1999								
F10	2	20	12	F	13	825	9.1	0.90
F11	3	17	12	F	0	790	7.7	0.83
F12	5	33	12	F	12	800	13.9	1.11
F14	8	18	12	M	0	835	11.5	1.01
F15	4	19	12	M	0	845	10.0	0.94
F16	5	18	12	M	0	811	10.6	0.97
F17*	3	15	6	F	0	666	9.6	1.31
F18*	3	19	6	F	0	660	13.7	1.56
F19*	3	11	6	F	0	697	6.8	1.10
F2*	3	15	6	F	1	760	8.1	1.21
F20*	8	18	6	F	0	862	12.1	1.47
F21*	6	18	6	M	0	785	10.9	1.40
F22*	5	12	6	F	0	840	7.8	1.18
F23*	3	12	6	M	0	733	7.8	1.18
F24*	3	12	6	F	7	855	6.3	1.06
F25	9	16	12	F	1	731	12.8	1.07
F26	9	24	10	F	16	860	14.1	1.21
F27*	3	14	5	M	0	728	6.8	1.18
F28	5	11	10	M	0	810	6.3	0.81
F29	8	22	10	F	0	535	11.8	1.10
F3*	7	17	6	F	8	840	9.8	1.32
F30	2	9	10	M	0	745	5.2	0.73
F31	4	12	10	M	0	745	6.4	0.81
F4	6	22	12	F	5	820	12.7	1.07
F5	4	32	12	F	4	800	8.5	0.87
F6	3	22	12	M	0	810	7.3	0.81
F7	2	11	12	F	0	760	5.7	0.71
F8	3	15	12	F	5	745	9.0	0.89
F9	6	24	12	F	3	780	11.6	1.02
K18	4	11	12	M	0	769	6.8	0.78
K19	3	16	12	M	0	762	7.1	0.79
K20	4	20	12	M	0	730	8.7	0.88
K21	6	19	12	F	0	675	9.7	0.93
K22	6	25	12	F	0	725	12.8	1.07
K23	8	21	12	F	0	726	13.7	1.11
K24	0	2	12	M	0	485	0.5	0.22
K25	7	29	12	M	0	840	14.0	1.12
K26	7	17	12	M	0	740	10.8	0.98
K27	9	26	12	F	6	760	13.1	1.08
K28	5	32	12	F	10	835	12.2	1.04
K29	8	19	12	M	0	832	11.4	1.01
K30	7	14	12	F	4	822	9.9	0.94
K31	5	20	12	M	0	820	10.8	0.98
K33	4	14	12	M	0	700	7.8	0.84
K34	4	14	12	F	6	788	9.0	0.89
K35	4	22	12	M	0	845	9.6	0.93
2000								
K10	6	18	12	F	12	835	10.2	0.95
K11	4	13	12	M	0	690	8.3	0.86
K12	8	22	12	M	0	810	12.1	1.04
K28	3	13	12	M	0	810	9.1	1.14
K29	0	5	12	F	0	540	1.7	0.90
K30*	7	11	6	M	0	815	8.5	1.23
K31*	6	10	6	F	0	880	7.8	1.18
K9	5	15	12	M	0	780	8.1	0.85

Central Atlantic								
Whale	Min.	Max.	*n*	Sex	Ov.	L(cm)	Est. age	SD Est.
1999								
K1	5	23	11	F	12	857	8.5	0.87
K10	6	13	12	F	5	845	10.0	0.95
K11*	7	13	6	F	0	705	10.4	1.36
K12	2	12	12	F	7	802	6.7	0.77
K13	4	12	12	F	18	855	7.5	0.82
K14	5	17	12	M	0	730	10.4	0.96
K15	9	19	6	F	4	858	11.3	1.42
K17	5	18	12	F	0	760	10.2	0.95
K2	7	16	12	F	9	840	10.2	0.95
K3	7	27	12	F	11	810	12.2	1.04
K4	9	14	12	F	15	885	11.1	0.99
K5	6	21	12	F	10	870	10.2	0.95
K6	8	13	12	F	3	776	9.4	0.91
K7	5	11	12	F	15	855	8.1	0.85
K8	4	11	12	F	10	801	7.2	0.80
K9	0	14	12	F	11	868	8.1	0.85
2000								
K1	4	16	12	M	0	747	8.8	0.89
K13*	4	10	6	M	0	585	7.3	1.14
K14*	3	13	6	F	0	700	8.0	1.19
K15*	7	14	6	F	0	765	8.3	1.22
K16*	9	22	6	F	0	765	12.2	1.48
K17*	13	21	6	F	0	770	16.7	1.72
K18*	10	13	6	F	0	848	11.6	1.44
K19*	7	11	6	F	0	670	9.0	1.26
K2	6	16	12	M	0	770	10.6	0.97
K20*	7	23	6	F	0	740	13.9	1.57
K22*	3	10	6	M	0	792	6.2	1.05
K23*	4	13	6	F	0	770	8.5	1.23
K24*	12	21	6	F	0	715	15.2	1.65
K25*	7	12	6	F	0	810	9.1	1.28
K26*	6	20	6	F	0	805	12.9	1.52
K27*	5	11	6	M	0	720	7.3	0.39
K3	5	13	12	M	0	712	7.2	0.80
K4	5	18	12	M	0	793	9.9	0.94
K5	5	17	12	F	1	725	10.9	0.98
K6	6	14	12	F	12	820	10.3	0.96
K7	6	13	12	M	0	735	8.8	0.89
K8	5	12	12	M	0	820	6.7	0.77

from each bulla, all within 1cm of each other. The three segments were mounted on one microscope-slide. All slides were randomly given new numbers to prevent the readers from recognising the slides between readings. Two readers aged each bulla segment independently, where each reader first read the first section of all bulla. The slides were then put away for 5-7 days, the slides were renumbered, and the readers proceeded to read the second and then the third segment with renumbering and rest in-between.

Previous studies have not indicated any morphological difference between the North Sea and Central Atlantic (Christensen *et al.*, 1990) and the data were therefore pooled from both areas. Using a modified Poisson model and GLMM regression (Olsen and Skaug, 2002) a single age estimate was made for each whale based on all readings from the particular animal. The model was also used to estimate the standard deviation of this estimate. The model estimated ages were compared with the body length and ovulations.

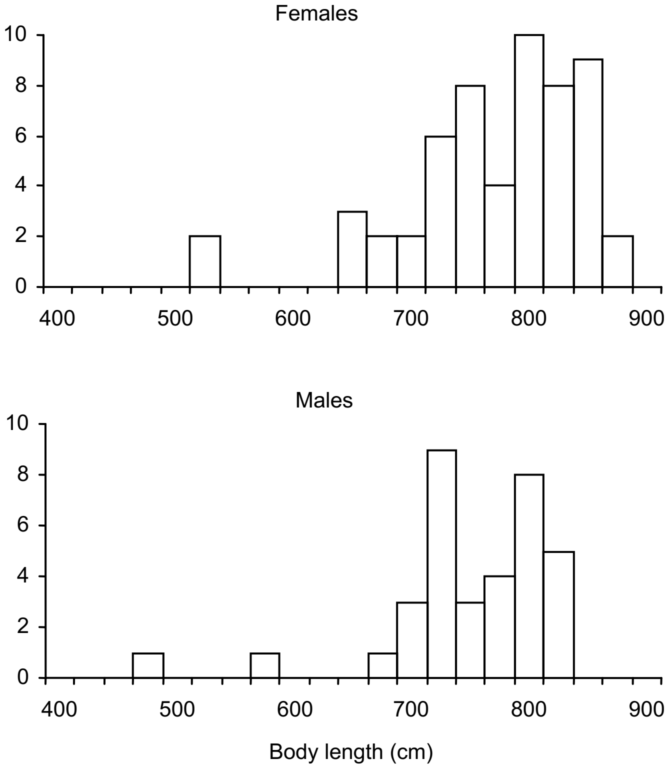

Fig. 3. Histograms of body length (cm) of male and female minke whales sampled in the North Sea and Central Atlantic in 1999 and 2000.

When analysing age versus ovulations a linear regression line was fitted to the plot to evaluate if there was a correlation and if there was a linear increase of one ovulation per year of age as might be expected. For the age versus length analysis, the sample was split into male and female sub-samples (since each sex shows a different growth pattern), a von Bertalanffy growth equation was fitted to the plot and L_{MAX}, k, and t_0 were estimated.

RESULTS

The length distribution of the sample is shown in Fig. 3, and as expected shows that females achieve longer maximum body lengths than the males. Samples from the smaller length groups ($<$ 650cm) were few, with only five females and two males. This is not representative of the population, but an artefact due to the size-selective catching by the whalers who have a set catch limit and wish to maximise the amount of meat. The sex ratio for the whole sample set was 38% males and 62% females. However splitting the sample by region revealed that in the North Sea, the sex ratio was 46% males and 54% females, whilst in the Central Atlantic it was 26% males and 74% females. The different sex ratios are probably not an artefact of the hunting, but rather a result of the sex-segregated migration of the species (Jonsgård, 1951).

Even with 28 whales missing one bulla completely, all whales in the sample were given at least six independent age estimates (three by each reader). For six whales, one of the readers was unsure about the estimate of a particular bulla segment and therefore did not age that particular segment.

Age estimates of single bulla segments ranged from 0-33 years respectively (Table 1), and the largest difference between minimum and maximum age estimates for an individual whale was 28 years (whale F5/1999). The standard deviation of the modelled age estimates ranged from 0.2-1.7, translating into 95% confidence intervals of the age estimates from ± (0.1-1.4) years. Plotting the coefficient of variation (CV) versus age (Fig. 4) showed a slight decrease in CV with age, except for the two youngest animals who had a markedly higher CV than the rest of the sample. As expected the whales with a missing bulla had a higher CV than the others.

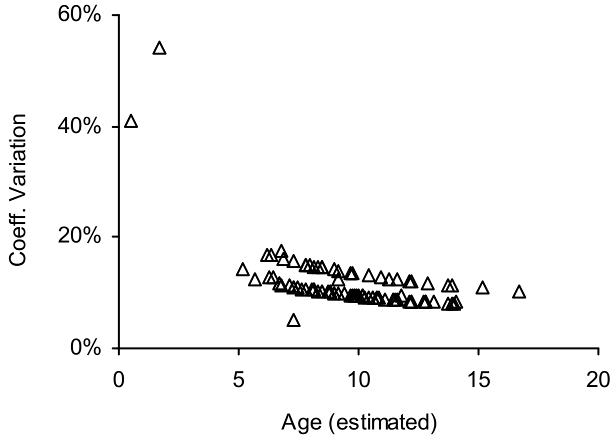

Fig. 4. Estimated age vs coefficient of variation of bulla age estimates from 57 female and 35 male minke whales. For 28 whales either the left or right bulla was missing, and this reduced the sample size for these whales by half, indicated in the plot by the points with higher CV than whales with similar age.

In the analysis of bias, no correlation was found between the estimated age and number of ovulations (Fig. 5, $R^2 = 0.001$) because the number of ovulations at a given estimated age ranged from 0 to ~ 15. This was contrary to expectations of a linear increase in number of ovulations after sexual maturity (see Fig. 1) and can only be explained by the bulla age underestimating true age. The underestimation was also apparent from the plot of residuals shown in Fig. 6 indicating a mean underestimation of 37% given ASM of eight years and 12% given ASM of four years.

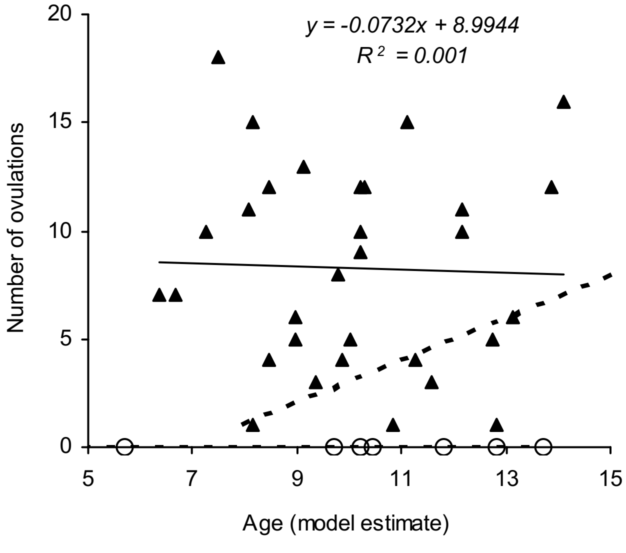

Fig. 5. Observed relationship between age and number of ovulations from 92 minke whales sampled in the North Sea and Central Atlantic in 1999 and 2000. A linear regression line is fitted to the whales with one or more ovulations (filled triangles) with regression equation and R^2 value is shown in the plot. The dashed line indicates the theoretical expected relationship given an annual ovulation rate and knifes-edge maturation at eight years. One immature whale estimate to one year of age is not shown.

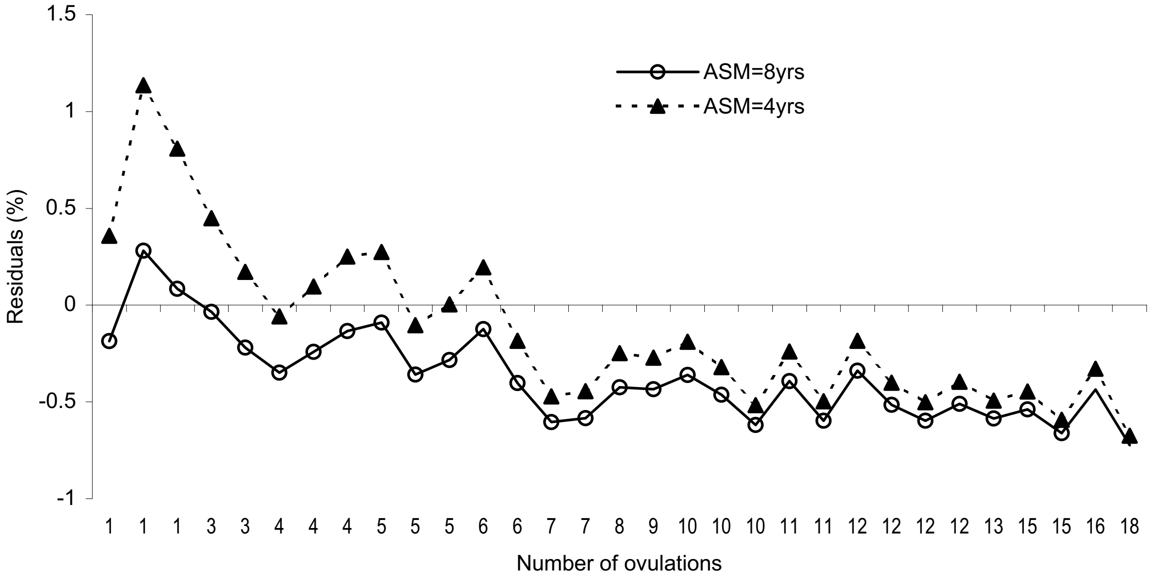

Fig. 6. Mean percentage residuals of the age estimates of individual whales when compared with the theoretical age estimated given annual ovulation rate and knifes-edge maturation at eight years (circles), or four years (triangles).

Using either assumed ASM indicated a progressive underestimation of age, with the youngest age classes being overestimated while the older being underestimates.

When plotting body length versus age (Fig. 7 and Fig. 8) it was found that the male sample seemed to fit the von Bertalanffy growth equation better than females. From Fig. 8 it can be seen that one whale is apparently an outlier (F29/1999), but removing this from the analysis did not notably improve or change the fit of the von Bertalanffy growth model. The curves were widely different for both sexes, which was apparent both from visual inspection and from comparing the model parameters (Table 2). These revealed that the males would grow to a larger size than females, but this was a result of different fit due to the lack of small animals and varying ages estimated for a give length class. Most whales in the sample were full-grown, or close to it, indicating little increase in size with age. Thus, the von Bertalanffy curves were driven by the few small and young animals in the samples introducing large differences between the sexes in model fit. In fact, the dataset encompassed only four animals less than 600cm long, and only one male and female was estimated to be less than five years of age.

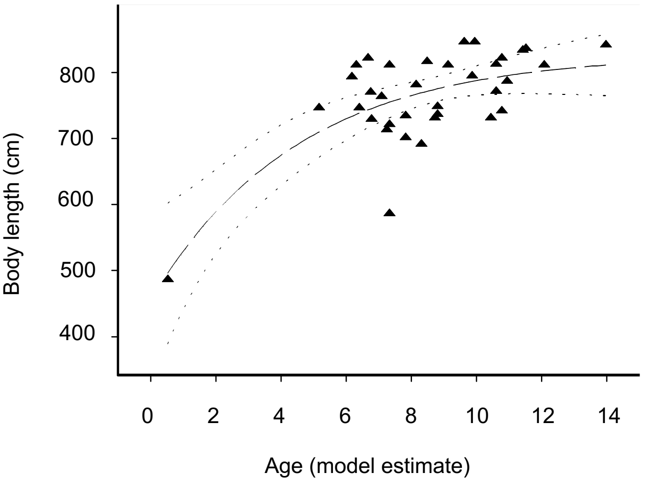

Fig. 7. Body length vs estimated age for 35 male, North Atlantic minke whales caught in 1999 and 2000. A von Bertalanffy growth equation with 95% confidence intervals is fitted to the data.

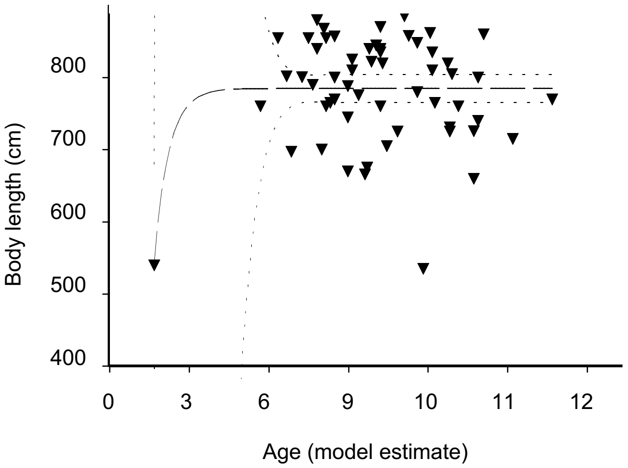

Fig. 8. Body length vs estimated age for 57 female, North Atlantic minke whales caught in 1999 and 2000. A von Bertalanffy growth equation with 95% confidence intervals is fitted to the data.

Table 2

Parameter estimates for the fitted von Bertalanffy growth equations in Figs 6 and 8. L_{MAX} is an estimate of mean maximum body length, k governs the growth rate while t_0 is a theoretical estimate of age at 0 length.

Sex	L_{MAX}	*k*	t_0
Males	827	0.22	-3.6
Females	785	1.81	1.0

DISCUSSION

An age determination method can only be useful in management if it yields fairly precise and unbiased estimates of true age without the need for resorting to accessory information to estimate age. In addition, the method must be applicable for both sexes and to most of the age-spectrum in the population. This investigation was devised with these considerations in mind, with all bulla age readings being blind readings, and attempting to use as representative a dataset as was possible to obtain. Few small whales (< 600cm body length) were included and any further study should attempt to sample more small whales. However, the sampled whales included females who had had 0-18 ovulations, corresponding to ages <7-25 years given an ASM of ~ 8 years (Olsen, 1997).

The precision estimated for the GLMM model age estimates ranged from ± (0.1-1.4) years (95% confidence interval), which was consistent with Christensen (1995) who found 80% agreement within ±1 year for three readers. Coefficients of variations decreased with increasing age (Fig. 4), and ranged from 5-14% for whales with ages >5 years based on 12 parallel readings. The sample included two animals with an estimated age of <2 years (K24/1999 and K29/2000). The ages of the other whales were estimated to be >5 years, making the two smallest outliers in the GLMM regression analysis, resulting in very high CVs for these two whales. The GLMM model suffered from a non-homogenous dataset, lacking equal dispersal of age estimates of the sampled whales. Even so, the mean CVs in the present study were larger than those found by (Kato *et al.*, 1991b) from two parallel readings of Antarctic minke whale earplugs, and indicate that the bulla method is less precise than the earplug method. The results here were based on 6-12 parallel readings, and Olsen and Skaug (2002) indicated that 2-8 parallel readings were necessary to reach ±2 years precision. Conducting this many parallel readings on all whales sampled from the Norwegian catch would require a much larger effort than is currently employed.

Even though the precision was reasonable, the analysis of bias did not follow the expectations illustrated in Fig. 1. In Fig. 5 the expected increase in ovulations with age was not found. With a R^2 of 0.0014 and whales as young as seven years having 18 ovarian scars, Fig. 5 indicated that the age estimates were underestimates of the true age. The plot of ovulations versus age in Fig. 1 is simplistic, ignoring age-specific ovulation rates. However, with no indication of change in ovulation rate of North Atlantic minke whales, the model is not unrealistic, but more research should be conducted on evaluating age-specific ovulation rates for the species. Fig. 1 shows that even with a density-dependent shift in ASM and ovulation rates varying from 0.5-2 per year an increase in the numbers of ovulations with increasing age would be expected if the age estimates were unbiased. Fig. 5 showed no such relationship, which leaves the conclusion that bulla age estimates are not representative of the true age, and are severely biased. The steady downward trend in the residuals (Fig. 6) further strengthens this conclusion, and high positive residuals for the youngest animals show that these were the most problematic to age. None of the modelled ages exceeded 15 years, which is low compared with Antarctic minke whales who have been shown to live for more than 30 years (Kato *et al.*, 1991a). Studies by Christensen (1981) and Olsen and Sunde (2002) also indicated that North Atlantic minke whales could live for more than 30 years, and that ages exceeding 15 years were common. This shows that it becomes progressively more difficult to detect the outermost GLGs of older animals. However, excluding animals with a modelled age >10 years would have little effect on the bias observed in Fig. 5, as Fig. 6 indicates a steady downward trend in bias through all age-classes. Some of the variability found in Fig. 5 may be due to variations in ovulation rate within the population, and individual differences in ASM. However, even with large variability in ovulation rate and ASM as explored in Fig. 1 some correlation between age and ovulations should be expected. Assuming that the model of one ovulation per year and ASM of eight years is correct, the residuals indicated an average underestimation of 37%, but ranging from an overestimation of 28% to an underestimation of 72%. However, without any known-age whales it is impossible to determine the exact magnitude of the bias.

Previous results on sexual dimorphism in length published by Christensen (1975), Jonsgård (1951), Larsen and Kapel (1982), Larsen and Kapel (1983), and Fig. 3 all show that females grow to larger sizes than males. When the von Bertalanffy growth model failed to achieve the same results (Fig. 7, Fig. 8) it was due to the clumped distribution of the data, the large variability in estimated age for a given length and the lack small animals which are crucial in fitting a von Bertalanffy curve correctly. The large difference in the k and t_0 parameters between the sexes (Table 2) also indicated that fitting the growth model was not successful. Even though there is sexual dimorphism in maximum body length, the length at birth and growth rate between the sexes should be very similar, and at least not as divergent as indicated from these analyses (Table 2).

The analysis of bias in this paper was based on an indirect approach since known-age animals or a validated ageing method for this species are missing. Therefore, the number of ovulations and body length were used as controls. These two parameters can themselves be subject to error, for instance the number of ovulations was determined from one examination of the ovaries by one reader. Few inconsistencies in their interpretation were expected, but a parallel ovary-examination study should be undertaken to verify this. Body length on the other hand has less potential error, but since the whales were measured at sea with head and tail sticking outside each side of the boat this might add some random error to the length measurements.

Reader variability was to a large extent the cause of the low precision (Olsen and Skaug, 2002), but the high bias is probably due to a combination of reader and biological effects. These biological effects are most probably the inconsistent nature of bulla GLG formation in the periosteal layer. The underestimation bias identified in the present analysis show that readable GLGs are not always formed in bulla every year. Adding to this basic uncertainty of GLG formation, the bulla GLGs observed were not continuous through a whole bulla section, but rather found at the peaks on small ridges or in cracks of the bulla. It is difficult to follow a single GLG through a single bulla segment, and almost impossible to find the same GLG in a segment cut only a few centimetres to either side of the first segment. In addition, many bulla GLGs are often very faint, thin and difficult to detect, while others are broad and clear. In some segments, a combination of thin and broad GLGs have been found making interpretation almost impossible. Bone resorption in bulla occurs along the mesosteal-periosteal interface (Christensen, 1981), and cannot explain the variable GLG widths and faintness observed in the outer parts of the periosteal layer. It does however explain why it is often difficult to identify the neonatal line in bulla segments. Adding to this confusion is the difficulty of determining where the neonatal line is and where post-parturition growth begins. These biological quirks makes a large degree of the bulla age determination procedure dependent on the subjective decisions of the reader and explains the lower precision and high bias of the bulla method compared to the earplug method.

From a management objective, the problem of precision in the bulla method is solvable through increasing the number of parallel readings of bulla segments from the same animal. However, the high bias will greatly limit any age-based monitoring of the North Atlantic minke whale population. The bias will tend to compress and level out even determinable age-classes (Bradford, 1991), making it impossible to monitor changes in age-dependent demographic parameters. It seems impossible to circumvent this bias in any way, and therefore other age determination methods, such as the aspartic acid racemisation technique (Olsen and Sunde, 2002) should be employed to age North Atlantic minke whales.

ACKNOWLEDGEMENTS

I wish to thank Arild Leithe and Bjørn Bergflødt for reading all the bulla segments, Hans J. Skaug for the GLMM modelling, Leif Nøttestad and Nils Øien for reviewing previous versions of the manuscript, and the crew and owners of M/S *Feie* and M/S *Kato* for cooperation and help during the sample collection. The comments of two reviewers are appreciated. This project was funded as part of Norwegian Research Council project number 127211/120.

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