AGE-SPECIFIC GROWTH AND REMARKABLE LONGEVITY IN NARWHALS (*MONODON MONOCEROS*) FROM WEST GREENLAND AS ESTIMATED BY ASPARTIC ACID RACEMIZATION

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Eyes from 75 narwhals (*Monodon monoceros*) were collected in West Greenland in 1993 and 2004 for the purpose of age estimation. Age estimates were based on the racemization of L-aspartic acid to D-aspartic acid in the nucleus of the eye lens. The ratio of D- and L-enantiomers was measured using high-performance liquid chromatography. The aspartic acid racemization rate (k_{Asp}) was estimated to be 0.001045/year $\pm$ 0.000069 *SE* by regression of D/L ratios on age estimated by length from 15 young narwhals ($\leq$298 cm) and by earplug laminations from 13 fin whales (*Balaenoptera physalus*). The D/L ratio at age 0 (($D/L)_0$) was estimated to be 0.0288 by regression of D/L ratios against the estimated age of the 15 young narwhals. The intercept of the regression slope, providing twice the ($D/L)_0$ value, was 0.05759 $\pm$ 0.00147 *SE*. The maximum estimated age was a 115-year-old ($\pm$10 *SE*) female. Asymptotic body length was estimated to be 396 cm for females and 457 cm for males, and asymptotic body mass was estimated to be 904 kg for females and 1,645 kg for males. Using the von Bertalanffy growth model, age at sexual maturity was estimated to be 6–7 years for females and 9 years for males.

Key words: age estimation, aspartic acid racemization, *Monodon monoceros*, narwhal

The narwhal (*Monodon monoceros*) is a toothed whale that reaches 4–5 m in length at physical maturity and is found year-round in Arctic waters mainly around Greenland and northern Canada. However, during the last 2 decades the West Greenland narwhal populations have experienced a population decline most likely attributable to increasingly intensive hunting (Heide-Jørgensen 2004; Heide-Jørgensen and Acquarone 2002). To ensure the best possible management and sustainable use of the narwhal populations, more biological knowledge of the species is needed. One key factor for studying a species' population dynamics is the availability of a reliable method for age determination of individuals. This is crucial for deriving the age structure of the population, for estimates of survival rates and age-specific reproductive parameters, as well as for assessing changes in life-history parameters caused by density dependence or environmental stress.

Reliable age estimation methods have not been developed for many whale species, including the narwhal (Hay 1980). Age determination of odontocetes has traditionally been performed by counting growth layer groups in the teeth. Validation has, in some cases, been done by reference to known-age animals in captivity (Hohn et al. 1989). However, the use of dentinal or mandibular growth layers has failed to provide reliable results for narwhals, especially in older individuals (Hay 1980). No narwhals have been successfully kept in captivity and there are no animals available with known age and life history. Thus, there is an urgent need for developing reliable techniques for revealing growth increments in narwhal tissue and, hence, their age.

The aspartic acid racemization technique was originally developed to assess ages of fossils and marine sediments (Bada et al. 1970; Bada and Protsch 1973; Wehmiller and Hare 1971). However, since the 1980s several studies have used the technique for age estimation of mammals, including whales and

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humans (Bada et al. 1980, 1983; George et al. 1999; Masters et al. 1977; Nerini 1983; Ohtani et al. 1995; Olsen and Sunde 2002). The method assumes that all amino acids, including aspartic acid, can exist in 2 different isomeric forms called L- and D-enantiomers. All of the amino acids normally incorporated into proteins in living organisms are of the L-form (Mathews and Van Holde 1996). In stable proteins, however, the L-form is slowly, and at a constant rate, converted to the D-form and the D/L ratio can thus potentially be used as a marker for age (Masters et al. 1977). The proteins in the nucleus of the eye lens are among the most stable in the mammalian body and subject to detectable racemization (Bada et al. 1980; George et al. 1999; Masters et al. 1978; Olsen and Sunde 2002). Because aspartic acid has the fastest racemization rate of the amino acids in body tissues (Bada and Schroeder 1975), it also is the most frequently used of the amino acids for age estimation of mammals. Racemization reactions of the amino acids are also temperature dependent, and increase with increasing temperature.

In our study, eye lens nuclei from 75 narwhals were used for age estimation. First, the usefulness of the aspartic acid racemization technique in estimating the ages of narwhals was examined, and 2nd, the estimated ages were used to describe age-specific growth and reproductive parameters for narwhals.

MATERIAL AND METHODS

Sampling.—Eyeballs from 75 narwhals were collected during the Inuit hunt of narwhals in Uummannaq and Qeqertarsuaq, West Greenland. Of the 75 whales, eyeballs from 52 whales were collected by employees from the Greenland Institute of Natural Resources in Uummannaq in November 1993. Eyes from 23 narwhals, 21 with both right and left eyeballs, were collected by the 1st author in Qeqertarsuaq, March 2004. A total of 48 individuals (64%) of the sampled whales were males, whereas 24 (32%) were females and 3 (4%) were of unknown sex. Body length was obtained for 63 individuals and body mass for 51. Eyes were frozen and stored at −20°C immediately after collection to halt further racemization. In the laboratory, lenses were dissected out of the eyes and lens layers surrounding the nucleus were removed by slowly rolling the lens on paper. All remaining layers were removed under a stereoscope. It is important not to contaminate the nucleus with younger lens layers or blood. Nuclei were cut in half for further analysis and kept frozen at −20°C.

Hydrolysis and high-performance liquid chromatography (HPLC).—Hydrolysis of the samples and the following HPLC analysis were performed following the procedures of Zhao and Bada (1995).

An Agilent 1100 Series HPLC system (Agilent Technologies, Walbronn, Germany) was used for the analysis. The system consisted of a degasser G1379A, a capillary pump G1376A, an autosampler ALS G1313A, a column compartment G1316 A, a fluorescence detector G1321A (operated at excitation = 340 nm, emission = 450 nm) and a multi-wavelength detector MWD G1365B. The column used was a Zorbax Eclipse XDB-C18, 4.6×150 mm, with particle size of 3.5 μm. The HPLC system was connected to a Chemstation Software system, version A.08.03 (Agilent Technologies). When preparing the OPA-NAC (*ortho*-phthaldialdehyde and N-acetyl-L-cysteine) a 0.1 M sodium borate buffer (pH 9.4) as suggested by Olsen and Sunde (2002) was used instead of the 0.4 M solution used by Zhao and Bada (1995). The use of sodium citrate (pH 5.6) as the buffering agent in the mobile phase instead of sodium acetate (Zhao and Bada 1995) improved the resolution between the diastereomeric derivatives of aspartic acid. This modification resulted in a better separation of the derivatives of D- and L-enantiomers of aspartic acid with no partial peak overlap facilitating a more correct integration of the peak areas as also suggested by Galindo et al. (2003).

For calibration of the D/L ratios measured by the HPLC, the following D/L standards (10^{-4} M) were prepared: 0.5/99.5, 1/99, 2/98, 5/95, 10/90, and 15/85, and run at the beginning and end of each HPLC run. For this purpose reference substances of L-aspartic acid and D,L-aspartic acid were used. The calibration standard solutions prepared were divided into a number of vials and kept at −20°C to be used in subsequent analyses. D- and L-aspartic acid peak areas were integrated automatically by the computer connected to the HPLC apparatus or manually if the peak areas were too small for the HPLC apparatus to integrate them, providing the ratio between the 2 enantiomers. Repeatability of the measured D/L-ratio of aspartic acid corresponding to 2% isomerization and expressed as the coefficient of variation was found to be 1.11% ($n = 6$; 2.0/98.0) and when analyzing the right and left eyes from a cow it was less than 1.7% ($n = 4$). The measured D/L ratios from the eye lens nuclei obtained by the HPLC were recalculated using the calibration equations (linear regression) for the D/L standards.

Estimating ages, the $(D/L)_0$ value and the racemization rate (k_{Asp}).—The age of an individual (A) is estimated according to the equation (George et al. 1999):

$$\hat{A} \text{ (years)} = \frac{\ln\left(\frac{1 + D/L}{1 - D/L}\right) - \ln\left(\frac{1 + (D/L)_0}{1 - (D/L)_0}\right)}{2k_{Asp}}$$
$$= bx - bx_0 = b(x - x_0), \qquad (1)$$

where D/L is the ratio between the peak integration values of D-aspartic acid and L-aspartic acid, $(D/L)_0$ is the estimated D/L value at the age of 0, and k_{Asp} is the racemization rate for aspartic acid. Further, $b = 1/(2k_{Asp})$, $x = \ln[(1 + D/L)/(1 - D/L)]$, and $x_0 = \ln\{[1 + (D/L)_0]/[1 - (D/L)_0]\}$.

The average D/L ratio of the 2 eyeballs was used from whales where both eyes were collected. The $(D/L)_0$ value was estimated from 15 young narwhals ($\leq$ 298 cm in length, including 2 near-term fetuses) that could be classified to age plotted against $\ln[(1 + D/L)/(1 - D/L)]$ (Masters et al. 1977).

The racemization rate of aspartic acid (k_{Asp}) and $(D/L)_0$ were estimated by means of a calibration line obtained by regressing empirical values of $\ln[(1 + D/L)/(1 - D/L)]$ against the corresponding ages, that is,

$$\ln\left(\frac{1 + \text{D/L}}{1 - \text{D/L}}\right) = x_0 + 2k_{\text{Asp}}A = \bar{x} + 2k_{\text{Asp}}(A - \bar{A}) \qquad (2)$$

where $\bar{A}$ is the average of the N values of A used for determining the calibration line, and $\bar{x}$ is found as $\bar{x} = x_0 + 2k_{\text{Asp}}\bar{A}$ or as the average of the N corresponding values of $x = \ln[(1 + \text{D/L})/(1 - \text{D/L})]$. $2k_{\text{Asp}}$ and x_0 were estimated as the slope and the intercept of the straight line, respectively. Data from 15 young narwhals supplemented by data from 13 fin whales (*Balaenoptera physalus*—Nerini 1983) were available for this analysis. Ages of narwhals were derived from length measurements and month of death, whereas ages of fin whales were based on earplug laminations (Nerini 1983). Because $(\text{D/L})_0$ is close to 0, $2(\text{D/L})_0$ is approximately equal to x_0. The term $(\text{D/L})_0$ includes the part of the D enantiomers already present at birth plus the racemization taking place when the samples are being hydrolyzed in HCl (Bada and Schroeder 1975).

To test the precision of HPLC measurements we compared D/L values obtained from the right and left eye from 21 whales using a nested analysis of variance (ANOVA; eyes were nested within individuals). A nested ANOVA (e.g., see Sokal and Rohlf 1995) allows 2 eyes of an individual to be regarded as replicates, which means that there must be no systematic difference between left and right eyes with respect to D/L values. A paired *t*-test was used to test the validity of this assumption.

Precision of estimated ages.—To calculate the variance associated with a new estimate of age, equation 2 is rewritten as $\hat{A} = bx - b(\bar{x} - 2k_{\text{Asp}}\bar{A}) = bx - b\bar{x} + \bar{A}$. Assuming the measurement error associated with A used for the calibration line to be negligible allows us to consider $\bar{A}$ as a constant. This means that the variance of $\hat{A}$ can be found as (e.g., see Colquhoun 1971):

$$V(\hat{A}) = V(bx - b\bar{x} + \bar{A}) = V(bx) + V(b\bar{x}) - 2\text{Cov}(bx, b\bar{x}).$$
$$(3)$$

Furthermore, because new values of x will be stochastically independent of $\bar{x}$, the covariance term of equation 3 becomes 0. Finally, because b is stochastically independent of both x and $\bar{x}$, equation 3 now becomes (based on the delta method described by Seber [1973]):

$$V(\hat{A}) = V(bx) + V(b\bar{x}) = x^2V(b) + b^2V(x) + V(b)V(x)$$
$$+ \bar{x}^2V(b) + b^2V(\bar{x}) + V(b)V(\bar{x})$$
$$= b^2V_x + (x^2 + \bar{x}^2)V_b + V_bV_x, \qquad (4)$$

where $V_b \equiv V(b)$ and $V_x \equiv V(x) + V(\bar{x})$. Note that equation 4 deviates from the corresponding equation given by George et al. (1999) in several respects. In their model, the sign of V_bV_x is negative and V_b is multiplied by x^2, whereas we multiply it by $x^2 + \bar{x}^2$. Finally, George et al. (1999) define V_x as $V_x \equiv V(x) + V(x_0)$. As a consequence, the model of George et al. (1999) is likely to underestimate the variance associated with estimation of ages compared with our estimates.

The values of $V(x)$ was estimated by means of the residual (i.e., within-individuals) variance s^2 obtained from a nested
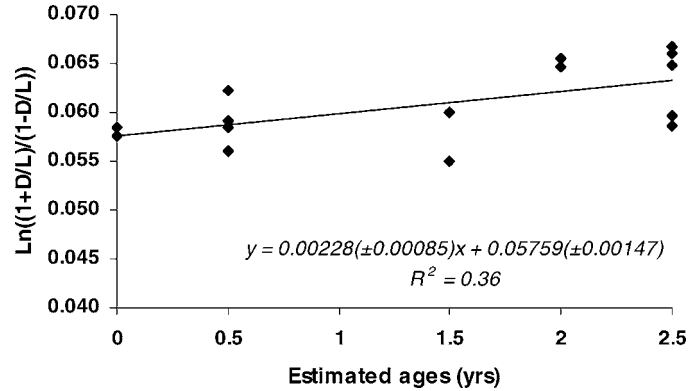

FIG. 1.—Regression of D/L ratio versus estimated age for 15 young narwhals ($\leq$298 cm) classified to age based on length and month of death (Appendix I). The intercept (0.05759) corresponds to twice the $(\text{D/L})_0$ value. The $(\text{D/L})_0$ value is thus 0.0288. The values in parentheses are *SE*s of estimated parameters.

ANOVA. This means that $V(x)$ in equation 4 can be found as $V(x) = s^2/n$, where n denotes the number of eyes examined from a given individual, that is, n is either 1 or 2. $V(\bar{x})$ is found as $V(\bar{x}) = s_r^2/N$, where s_r^2 is the residual variance obtained from the calibration line. Finally, V_b is found as (see Colquhoun 1971) $V_b = V[1/(2k_{\text{Asp}})] \approx (2k_{\text{Asp}})^{-4}V(2k_{\text{Asp}})$, where $V(2k_{\text{Asp}}) = s_r^2/\sum_{i=1}^{N}(A_i - \bar{A})^2$. Standard errors (*SE*s) of the individual age estimates were obtained as the square root of $V(\hat{A})$.

The von Bertalanffy and Gompertz growth models.—Standard length (L) and tusk length of whales were fitted to age estimates by the von Bertalanffy growth model (George et al. 1999; Olsen and Sunde 2002; von Bertalanffy 1938):

$$L = L_{\max}(1 - be^{-q\hat{A}}), \qquad (5)$$

where $L_{\max}$ is the asymptotic standard length and b and q are model constants to be derived. Similarly, the body mass (M) of whales was fitted to age estimates by the Gompertz growth model (Heide-Jørgensen and Teilmann 1994):

$$M = M_{\max}[\exp(-be^{-q\hat{A}})]. \qquad (6)$$

Least-square estimation of parameters was carried out in S-PLUS version 6.2 for Windows (Insightful Corp. 2003). Significance of statistical tests was determined at the level of $P < 0.05$.

RESULTS

Standard curves and linear regression equations.—Standard curves were produced using the D/L standards described above (e.g., 2 for each HPLC run) and linear regression equations were calculated by regression of theoretical versus measured D/L standards. We obtained a minimum $R^2 = 0.998$ for all the HPLC runs. For each HPLC run, the linear regression equation with a slope closest to 1 were chosen for recalculation of the D/L ratios obtained for the samples (range of slopes: 0.968–1.179).

Estimating $(\text{D/L})_0$ and $2k_{\text{Asp}}$ for aspartic acid.—Fifteen young whales were classified into age groups (with 0.5-year
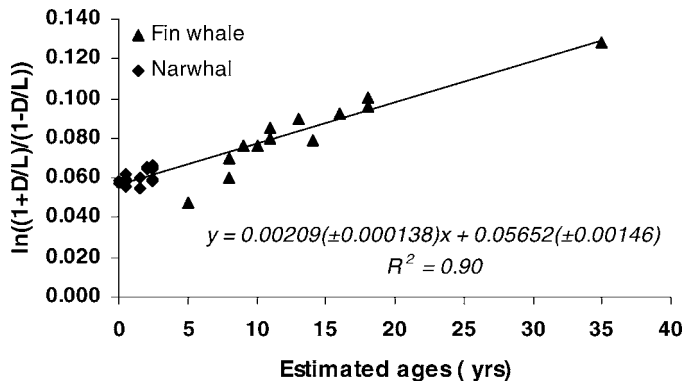
FIG. 2.—Regression of D/L ratio against estimated age for 15 narwhals and 13 fin whales. The 15 young narwhals were classified to age based on length and month of death (Appendix I; Fig. 1). The age estimates of the 13 fin whales were based on earplug laminations (Nerini 1983). The slope of 0.00209 corresponds to $2k_{Asp}$. Values in parentheses are *SE*s of estimated parameters.

intervals) based on their length, mass, and the month of capture (Appendix I). The individual values of $\ln[(1 + D/L)/(1 - D/L)]$ were correlated with the corresponding age estimates and the derived value of 0.05759 ± 0.00147 *SE* corresponds to a $(D/L)_0$ value of 0.0288, specific to narwhals (Fig. 1). The value of 0.05759 was used for calculating ages for the narwhals >2.5 years.

The estimate of $2k_{Asp}$ was obtained using 15 young narwhals (Appendix I) supplemented by data for 13 fin whales from Nerini (1983). Estimated ages of narwhals and fin whales were plotted against $\ln[(1 + D/L)/(1 - D/L)]$ to derive a $2k_{Asp}$ of 0.00209/year ± 0.000138 *SE* (Fig. 2), which means that $k_{Asp} = 0.001045 \pm 0.000069$/year.

For 21 of the 75 whales both eyes were collected. A paired *t*-test showed no significant difference ($t = 0.23$, *d.f.* = 20, $P = 0.82$) between the D/L ratios of the left and right eyes.

Age estimates and associated SEs.—The residual variance of the calibration line (s_r^2) was 1.004×10^{-5}. Hence, $V(\bar{x}) = s_r^2/N = 6.692 \times 10^{-7}$ (Table 1).

The slope of the line fitted to the 28 values of $\ln[(1 + D/L)/(1 - D/L)]$ plotted against age (Fig. 2) had an *SE* of 0.000138,

TABLE 1.—Terms used for estimation of whale age and its *SE* (n = number of eyes examined per individual).

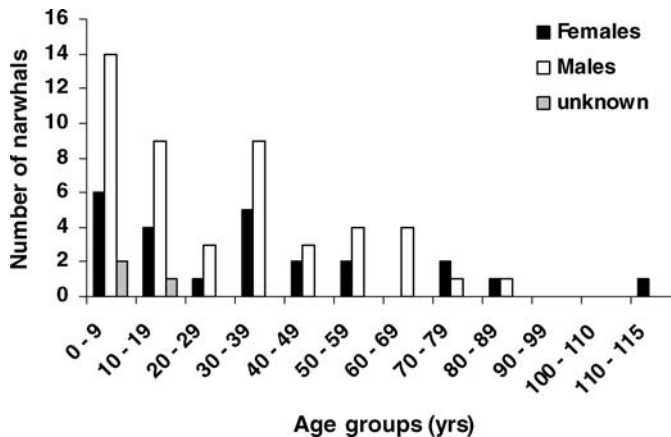| Parameter description	Term	Value
Slope of calibration line	$2k_{Asp}$	0.00209
Intercept of calibration line	x_0	0.05759
Average value of $x = \ln\left(\frac{1 + D/L}{1 - D/L}\right)$	$\bar{x}$	0.06085
Slope of prediction line	$b = \frac{1}{2k_{Asp}}$	478.94
Variance of $\bar{x}$	$V(\bar{x})$	6.692×10^{-7}
Variance of $2k_{Asp}$	$V(2k_{Asp})$	1.916×10^{-8}
Variance of b	V_b	1,008.37
Variance of a new x	$V(x) = s^2/n$	4.672×10^{-5} ($n = 1$)
		2.336×10^{-5} ($n = 2$)
V_x	$V(x) + V(\bar{x})$	4.739×10^{-5} ($n = 1$)
		2.403×10^{-5} ($n = 2$)

FIG. 3.—Age distribution in groups of 10 years of the 75 narwhals used in this study. Average ages of females and males are 34.7 and 27.4 years, respectively.

which means that $V(2k_{Asp}) = 1.916 \times 10^{-8} \cdot V_b = V[1/(2k_{Asp})]$, therefore, becomes $V_b = 1,008.37$ (Table 1).

The nested ANOVA showed that 98.6% of the total variation in the 42 observed values of $x = \ln[(1 + D/L)/(1 - D/L)]$ was due to differences between individuals, whereas the remaining 1.4% could be attributed to variation between eyes sampled from the same individual (measurement noise). The between-individuals variance ($s_{between}^2 = 0.003512$) was significantly ($F = 75.2$, *d.f.* = 20, 21, $P < 0.0001$) higher than the within-individuals variance ($s^2 = 4.672 \times 10^{-5}$; Appendix II). This means that $V(x) = s^2/n$ is 4.672×10^{-5} if x is based on a single measurement and 2.336×10^{-5} when x represents an average of 2 eyes. Likewise, $V_x = V(x) + V(\bar{x})$ is 4.739×10^{-5} for a single measurement and 2.403×10^{-5} for a double measurement (Table 1).

Since all terms except x in equation 4 can be regarded as constants, $V(\hat{A})$ can be written as $V(\hat{A}) = C + x^2V_b$, where $C = b^2V_x + \bar{x}^2V^b + V_bV_x$, which means that $C = 14.652$ when $n = 1$ and $C = 9.193$ when $n = 2$. Standard error of $\hat{A}$ therefore becomes $SE(\hat{A}) = \sqrt{C + x^2V_b}$, which shows that *SE* increases almost proportionally with x and therefore also with age.

Length- and mass-at-age.—A total of 75 narwhals provided age estimates by means of the aspartic acid racemization method (Appendix I; Fig. 3). About 20% of the sampled whales were estimated to be older than 50 years and maximum age calculated was a 115 ± 10-year-old female.

The von Bertalanffy growth model (equation 5) showed that the asymptotic body length of female and male narwhals is predicted to be 396 cm (95% confidence interval [95% *CI*]: 387–405 cm) and 457 cm (95% *CI*: 443–471 cm), respectively, and the asymptotic length is attained at an age of approximately 21 years for females and 26 years for males (Fig. 4). From the Gompertz growth model (equation 6) we estimated that asymptotic mass is 904 kg (95% *CI*: 812–996 kg) and 1,645 kg (95% *CI*: 1,532–1,755 kg) for females and males, respectively, and the asymptotic mass is attained at an age of approximately 37 years for females and 50 years for males (Fig. 4). External growth of the tusk reaches asymptotic length at 178 cm (95% *CI*: 161–196 cm) at approximately 53 years (Fig. 4).
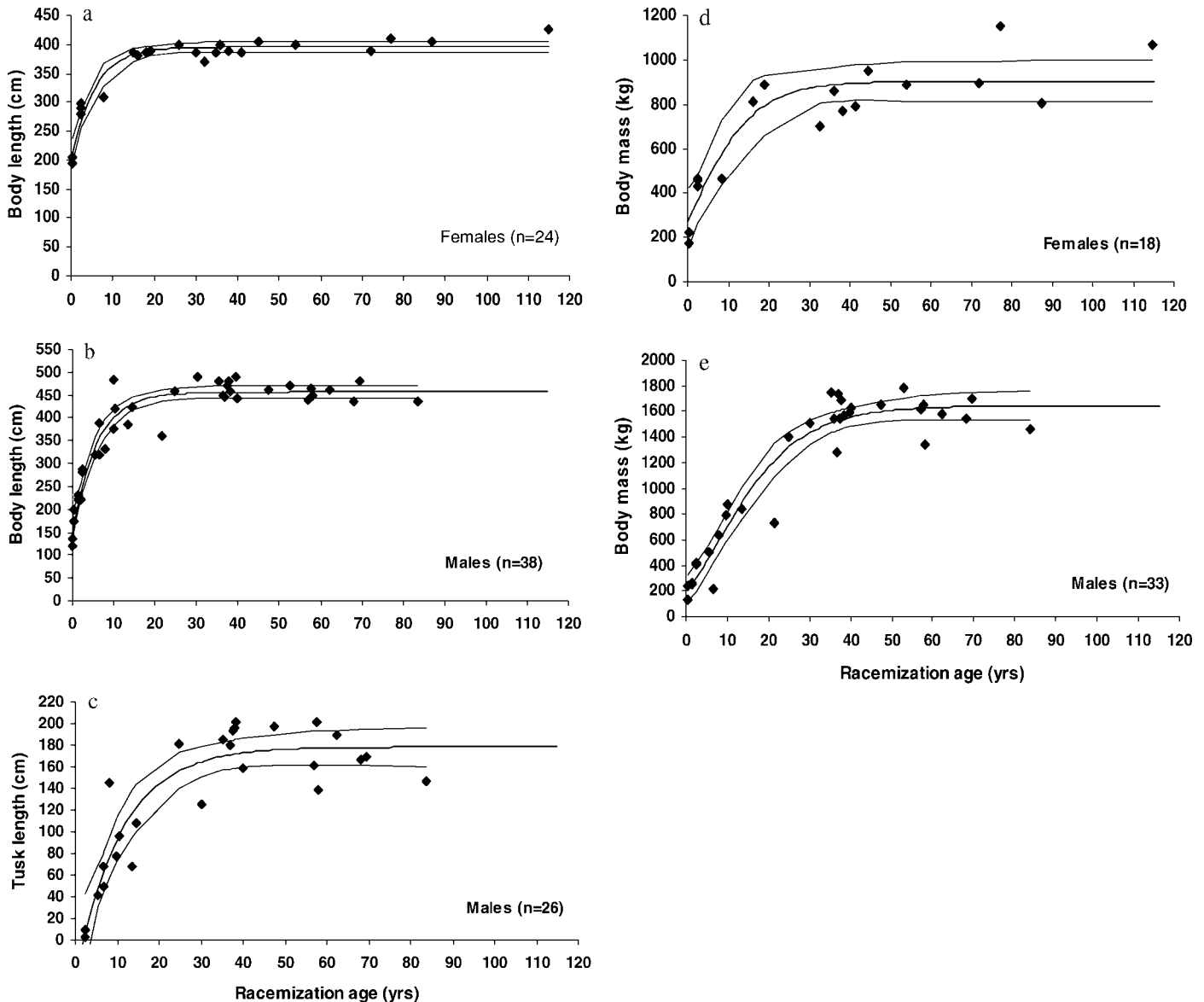
FIG. 4.—Growth in female and male narwhals. a, b) Body length curves and c) tusk length curve are fitted to a von Bertalanffy model. d, e) Body mass curves are fitted to a Gompertz model. The dotted lines are 95% confidence intervals (95% *CI*s).

We used the 15 young narwhals estimated to age based on their length and month of death in the growth models (Fig. 4) and recognize the circularity in this approach. However, randomly excluding half of the young narwhals with ages based on length and using the other half with aspartic acid racemization age estimates in the growth models did not change the growth curves and the results of the life history parameters significantly ($t = -1.262$, $d.f. = 4$, $P = 0.28$). We therefore decided to keep the original growth curves as shown in Fig. 4.

DISCUSSION

Aspartic Acid Racemization Technique

Racemization rate and (D/L)$_0$ *value.*—Based on 2 small (but not perinatal) minke whales (*Balaenoptera acutorostrata*; <7 m in length) Olsen and Sunde (2002) found a (D/L)$_0$ value of 0.0291. This is close to the value of 0.0285 derived by George et al. (1999) for bowhead whales (*Balaena mysticetus*), whose age was estimated to be less than 2 years based on baleen length. Rosa et al. (2004) used 2 bowhead whale fetuses to estimate a (D/L)$_0$ of 0.027. All these values are close to the value for narwhals estimated in our study of (D/L)$_0$ = 0.0288 (Fig. 1).

In general, racemization rates should not differ significantly between different warm-blooded animal species (Bada et al. 1980; George et al. 1999; Zhao and Bada 1995) justifying our use of data from 2 different whale species, the fin whale and the narwhal, for estimation of the racemization rate. The rate determined in our study ($2k_{Asp} = 0.00209$) is close to values from humans ($2k_{Asp} = 0.0025$), fin whales ($2k_{Asp} = 0.002209$), and the average of fin whales and humans used by George et al. (1999) for calculating bowhead whale age ($2k_{Asp} = 0.00235$). The $2k_{Asp}$ of 0.00209 derived from the narwhal and fin whale data is slightly lower than the sole fin whale rate and the human

TABLE 2.—Longevity, mean adult body length, age at sexual maturity, and mean annual calving intervals for selected cetaceans.

Whale species	Maximum age (years)	Mean adult body length (m) (F/M)[a]	Age at sexual maturity (years) (F/M)[a]	Mean annual calving intervals (years)	Reference[b]
Toothed whales (Odontocetes)					
Narwhal (*Monodon monoceros*)	115	4/4.75	6−7/9	3	1, 2
Killer whale (*Orcinus orca*)	90	9/7.7	12−16/15	3	3, 4
Sperm whale (*Physeter catodon*)	70	10.6/16	9/20+	5	5, 6
Short-finned pilot whale (*Globicephala macrorhynchus*)	63	6	9/13−16	3−10	5, 7
Long-finned pilot whale (*Globicephala melas*)	55	6	8/12	3.3+	5, 7, 8
Beluga (*Delphinapterus leucas*)	30	5	4−7/8−9	3	9
Baleen whales (Mysticeti)					
Bowhead whale (*Balaena mysticetus*)	211	16−18/14−17	25	3−4	5, 10
Fin whale (*Balaenoptera physalus*)	100	20/18.5	7−8/6−7	2−3	5, 11, 12
Blue whale (*Balaenoptera musculus*)	90	26.5/25	8−10	2−3	5, 13
Gray whale (*Eschrichtius robustus*)	80	14.1/13	6−12	2	14
Sei whale (*Balaenoptera borealis*)	60	15	6−10	2	15, 16
Humpback whale (*Megaptera novaeangliae*)	48	14−15	5	2	17, 18
Minke whale (*Balaenoptera acutorostrata*)	47	8.5/7.8	6/7	1	19, 20

[a] F = female; M = male.

[b] 1 = Present study; 2 = Heide-Jørgensen 2002; 3 = Olesiuk et al. 1990; 4 = Ford 2002; 5 = Evans 1987; 6 = Whitehead 2002; 7 = Olsen and Reilley 2002; 8 = Bloch and Lockyer 1993; 9 = Heide-Jørgensen and Teilmann 1994; 10 = George et al. 1999; 11 = Lockyer and Sigurjónsson 1992; 12 = Aguilar 2002; 13 = Sears 2002; 14 = Jones and Swartz 2002; 15 = Gambell 1985; 16 = Horwood 2002; 17 = Clapham 2002; 18 = Winn and Reichley 1985; 19 = Olsen and Sunde 2002; 20 = Perrin and Brownell 2002.

rate. The small differences in the rates might reflect lower temperatures in the eyes of these cold-water whales.

Standard errors of age estimates.—The *SE*s of the age estimates for younger whales obtained in this study are in the same range as *SE*s obtained by George et al. (1999) and Olsen and Sunde (2002). Rosa et al. (2004) found larger *SE*s for young whales caused by a larger variation of the paired eye lens data. *SE*s of the older whales in this study are about the same as in Olsen and Sunde (2002), but considerably lower than *SE*s from George et al. (1999) and Rosa et al. (2004). This is in spite of the circumstance that we used a formula that gives a higher *SE* than the one proposed by George et al. (1999). Thus, the smaller *SE* in our material is due to the individual variance components being smaller, which at least partly can be attributed to the fact that our sample size was larger than that of George et al. (1999).

Age estimates of older whales have a larger *SE* than those of younger whales but are more precisely aged in a relative sense (Appendix I). Error in the V_x term and $2k_{Asp}$ accounts for most of the variability in age estimates of young and old whales, respectively. Further sample collection of near-term fetuses to strengthen the $(D/L)_0$ estimates and repeated measurements of both eyes would reduce the *SE*s of especially the young whales. Although difficult to obtain, examination of more data from known age animals will clearly also reduce the uncertainty associated with $2k_{Asp}$.

Despite the rather large *SE*s associated with age estimates, the estimated ages may still be used to analyze various life history parameters in narwhals.

Biological Parameters

Growth and age at sexual and physical maturity.—Few studies on age-specific growth in narwhals have previously been conducted because of the lack of a reliable age estimation method, and the results presented here are thus among the 1st

to be published. The length at physical maturity was found to be 396 cm for females and 457 cm for males. Laws (1956) estimated that cetaceans attain sexual maturity at about 85% of their physical maturity. This corresponds to 337 cm or 6–7 years for females and 388 cm or 9 years for males. Length at sexual maturity is close to results from Hay (1984), who, based on examination of reproductive organs, estimated length at sexual and physical maturity, respectively, to be 340 cm and 415 cm for females and 395 cm and 470 cm for males. Hay (1984) estimated that female narwhals will reach sexual maturity at approximately 12 growth layers. The number of annual layering of growth layer groups in narwal teeth is not known (Hay 1984). However, findings for the beluga (*Delphinapterus leucas*), a close relative to narwhals, suggest that 2 layers/year are laid down (Goren et al. 1987; Heide-Jørgensen et al. 1994). If this also applies to narwhals, the findings of Hay (1984) would be in agreement with our results. In the study of Robeck et al. (2005), 1st conception of female belugas took place at an age of 6 years and the youngest male to sire a calf was 9 years old. A number of other studies have reported age at sexual maturity in belugas to range from 4 to 7 years for females and from 6 to 9 years in males (in Heide-Jørgensen and Teilmann 1994). All these findings are in accordance with our results for the narwhal.

Longevity in whales.—The aspartic acid racemization technique is the 1st and only to provide data on the longevity of the narwhal. Bada et al. (1983) found a maximum age of 52 years in a sample of 4 narwhals estimated via aspartic acid racemization in teeth, and Hay (1984) estimated maximum age to 45–50 years based on counts of mandibular periosteal layers. The maximum ages achieved in this study of 115 ± 10 years and 84 ± 9 years for females and males, respectively, are obtained from samples from a heavily hunted population of narwhals off West Greenland. The maximum age in other narwhal populations with less disturbed age structure might be

considerably higher. Maximum age also is likely to increase when more specimens are examined.

Longevity has been estimated for a number of whale species (Table 2). Some of the large baleen whales, such as the blue whale (*Balaenoptera musculus*) and the fin whale, can apparently live for 90–100 years (Lockyer and Sigurjónsson 1992; Sears 2002). Recently, it was discovered by use of the aspartic acid racemizaton technique that bowhead whales can live as long as 211 years (George et al. 1999) and thereby have the highest known longevity of the cetaceans. Among the toothed whales, only killer whales (*Orcinus orca*) may attain similar long life spans, reaching ages of up to 90 years. Even the large sperm whale (*Physeter catodon*) seems to have a shorter life span. However, it is important to realize that the estimated longevity of these other odontocetes is based on readings of dental growth layers usually without validation from known-age individuals. This, in combination with possible resorption of dental growth layers, may introduce a downward bias in the estimates of longevity by traditional methods (Evans et al. 2002; Hohn and Fernandez 1999; Myrick et al. 1988). Age obtained by the aspartic acid racemization technique would be overestimated if the whale had cataracts (brunnescent group IV—Masters et al. 1977, 1978), but so far cataracts have not been reported in the long-living bowhead whale (George et al. 1999) and no information of the possible development of cataracts in the narwhal eye has been published. Based on our data it seems likely that the narwhal is among the cetaceans with the highest longevity.

Old age—adaptation to a variable climate?—The narwhal, the bowhead whale, and the beluga are the only 3 cetaceans living year-round in Arctic waters and it is worth noting that 2 of these 3 Arctic cetaceans have considerably longer life spans than most of their relatives from lower latitudes (Table 2). Narwhals live in close association with the sea ice and during winter their survival depends on areas with sufficient open leads and cracks, which makes them susceptible to changes in sea ice regimes (Heide-Jørgensen et al. 2003). In the past, large climate changes in the Arctic areas have occurred on timescales of sometimes decades and perhaps even within a few years (Adams et al. 1999). Palsbøll et al. (1997) showed very low genetic diversity in narwhals from Canada, West Greenland, and East Greenland, resembling that seen in severely depleted whale stocks. The reason could be a result of historic population bottlenecks likely caused by dramatic habitat changes, for example by rapid changes in sea surface temperatures in the North Atlantic soon after the last deglaciation (Greenland Ice-Core Project [GRIP] Members 1993; Johnsen et al. 1992; North Greenland Ice Core Project Members 2004). One evolutionary strategy to overcome such sudden changes in climate could be high longevity, thus ageing could evolve as part of an optimal life history (Partridge and Barton 1993). The longevity of narwhals could therefore be seen as an adaptation to mitigate the population effects of drastic changes in climate.

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APPENDIX I

Basic data for the 75 narwhals (32% females, 64% males, 4% unknown sex) used in this study.[a]

Whale no.	Date of collection	Area[b]	Sex[c]	Mass (kg)	Length (cm)	Tusk length (cm)	D/L	Age (years)	SE	Relative error	No. eyes
Q1	17 March 2004	Q	M	—	—	—	0.0424	13.1	4.7	0.36	1
Q2	17 March 2004	Q	M	—	—	—	0.0505	20.8	5.0	0.24	1
Q3	17 March 2004	Q	M	—	—	—	0.0483	18.7	4.3	0.23	2
Q4	17 March 2004	Q	M	—	—	—	0.0388	9.6	3.9	0.41	2
Q5	17 March 2004	Q	—	—	—	—	0.0429	13.5	4.1	0.30	2
Q6	17 March 2004	Q	M	—	—	—	0.1029	71.3	7.2	0.10	2
Q7	17 March 2004	Q	M	—	—	—	0.0471	17.5	4.3	0.24	2
Q8	17 March 2004	Q	M	—	—	—	0.0649	34.6	5.1	0.15	2
Q9	17 March 2004	Q	M	—	—	—	0.0920	60.8	6.6	0.11	2
Q10	17 March 2004	Q	M	—	—	—	0.0331	4.1	3.7	0.89	2
Q11	17 March 2004	Q	M	—	390	67.5	0.0357	6.6	3.8	0.57	2
Q12	17 March 2004	Q	F	—	385	—	0.0448	15.3	4.2	0.27	2
Q13	17 March 2004	Q	M	—	420	96	0.0397	10.4	3.9	0.38	2
Q14	17 March 2004	Q	F	—	385	—	0.0477	18.1	4.3	0.24	2
Q15	17 March 2004	Q	M	—	135	—	0.0292	0	—	—	2
Q16	17 March 2004	Q	M	—	119	—	0.0288	0	—	—	2
Q18	17 March 2004	Q	F	—	385	—	0.0600	30.0	4.9	0.16	2
Q19	17 March 2004	Q	F	—	385	—	0.0654	35.1	5.1	0.15	2
Q20	17 March 2004	Q	M	—	425	108	0.0440	14.6	4.1	0.28	2
Q21	17 March 2004	Q	—	—	226	—	0.0327	2	—	—	2
Q22	17 March 2004	Q	M	—	220	—	0.0323	2	—	—	2
Q23	17 March 2004	Q	F	—	400	—	0.0849	53.9	6.2	0.11	2
Q24	17 March 2004	Q	F	—	400	—	0.0559	26.0	4.7	0.18	2
485	3 November 1993	U	M	1,285	450	—	0.0669	36.6	5.7	0.16	1
486	3 November 1993	U	M	1,402	458	182	0.0547	24.8	5.2	0.21	1
488	5 November 1993	U	M	630	333	145	0.0372	8.0	4.5	0.56	1
489	5 November 1993	U	M	1,567	457	201	0.0687	38.3	5.8	0.15	1
490	5 November 1993	U	M	1,648	465	202	0.0889	57.7	6.8	0.12	1
491	5 November 1993	U	M	1,539	435	167	0.0996	68.1	7.4	0.11	1
492	5 November 1993	U	M	1,581	460	189	0.0937	62.3	7.1	0.11	1
493	5 November 1993	U	M	1,789	470	—	0.0837	52.8	6.6	0.12	1
494	7 November 1993	U	F	468	290	—	0.0330	2.5	—	—	1
495	8 November 1993	U	M	1,345	450	139	0.0892	58.0	6.8	0.12	1
496	8 November 1993	U	M	1,706	480	170	0.1010	69.5	7.5	0.11	1
497	8 November 1993	U	M	1,749	480	185	0.0657	35.4	5.7	0.16	1
498	—	U	—	—			0.0369	7.8	4.5	0.58	1
499	9 November 1993	U	F	888	389	—	0.0486	19.0	4.9	0.26	1
500	9 November 1993	U	M	508	320	42	0.0345	5.5	4.4	0.80	1
530	11 November 1993	U	F	431	298	—	0.0293	2.5	—	—	1
531	14 November 1993	U	M	1,620	440	162	0.0881	57.0	6.8	0.12	1
532	14 November 1993	U	M	1,458	435	147	0.1156	83.6	8.3	0.10	1
533	15 November 1993	U	F	802	405	—	0.1196	87.4	8.5	0.10	1
534	15 November 1993	U	F	789	385	—	0.0720	41.4	6.0	0.14	1
535	15 November 1993	U	M	252	220	—	0.0275	1.5	—	—	1
536	15 November 1993	U	M	261	230	—	0.0300	1.5	—	—	1
537	15 November 1993	U	F	888	400	—	0.0852	54.2	6.6	0.12	1
538	18 November 1993	U	M	129	175	—	0.0280	0.5	—	—	1
539	18 November 1993	U	F	949	405	—	0.0753	44.7	6.1	0.14	1
540	18 November 1993	U	M	792	375	77	0.0390	9.8	4.6	0.46	1
541	18 November 1993	U	F	462	310	—	0.0376	8.5	4.5	0.53	1

APPENDIX I.—Continued.

Whale no.	Date of collection	Area[b]	Sex[c]	Mass (kg)	Length (cm)	Tusk length (cm)	D/L	Age (years)	SE	Relative error	No. eyes
542	18 November 1993	U	M	1,658	460	198	0.0781	47.4	6.3	0.13	1
543	18 November 1993	U	M	1,549	470	194	0.0679	37.5	5.8	0.15	1
544	18 November 1993	U	M	419	287	10	0.0324	2.5	4.3	—	1
545	18 November 1993	U	F	223	205	—	0.0292	0.5	4.2	—	1
546	18 November 1993	U	F	768	390	—	0.0687	38.3	5.8	0.15	1
547	18 November 1993	U	M	838	385	68?	0.0428	13.5	4.7	0.35	1
548	18 November 1993	U	F	700	370	—	0.0627	32.5	5.5	0.17	1
549	18 November 1993	U	M	214	320	50	0.0358	6.7	4.4	0.67	1
550	18 November 1993	U	F	461	280	—	0.0333	2.5	4.4	—	1
551	09 November 1993	U	M	238	198	—	0.0296	0.5	4.3	—	1
552	09 November 1993	U	M	1,588	490	—	0.0701	39.6	5.9	0.15	1
553	09 November 1993	U	F	814	380	—	0.0455	16.0	4.8	0.30	1
554	09 November 1993	U	M	1,739	445	180	0.0673	36.9	5.7	0.16	1
555	09 November 1993	U	M	729	360	—	0.0513	21.6	5.0	0.23	1
556	09 November 1993	U	M	1,539	—	—	0.0663	36.0	5.7	0.16	1
557	09 November 1993	U	M	409	280	3	0.0298	2.5	4.3	—	1
558	09 November 1993	U	M	1,688	480	196	0.0682	37.8	5.8	0.15	1
559	11 November 1993	U	F	896	390	—	0.1037	72.0	7.6	0.11	1
560	11 November 1993	U	F	1,148	410	—	0.1089	77.1	7.9	0.10	1
561	09 November 1993	U	M	1,629	443	159	0.0704	39.9	5.9	0.15	1
562	11 November 1993	U	F	1,068	425	—	0.1476	114.8	10.2	0.09	1
563	11 November 1993	U	F	170	195	—	0.0311	0.5	4.3	—	1
564	11 November 1993	U	M	1,509	490	125	0.0602	30.1	5.4	0.18	1
565	11 November 1993	U	F	858	400	—	0.0663	36.0	5.7	0.16	1
567	11 November 1993	U	M	878	485	—	0.0393	10.1	4.6	0.45	1

[a] Data for 15 young narwhals that are aged based on length and month of death are underlined.
[b] Q = Qeqertarsuaq, West Greenland; U = Uummaannaq, West Greenland.
[c] M = male; F = female.

APPENDIX II

Data from left and right eyes for 21 whales used in a nested ANOVA model for calculation of $V(x)$. $N = 21$ individuals, $n = 2$ eyes.

Whale no.	Sex[a]	1st eye: $\ln\left(\frac{1 + D/L}{1 - D/L}\right)$	2nd eye: $\ln\left(\frac{1 + D/L}{1 - D/L}\right)$	Average (1st and 2nd eye)	$s^2 = \sum_{i=1}^{N} \sum_{j=1}^{n} \frac{(x_{ij} - \bar{x}_i)^2}{N(n-1)}$
Q3	M	0.09733	0.09605	0.09669	3.90×10^{-8}
Q4	M	0.07908	0.07629	0.07769	1.85×10^{-7}
Q5	—	0.08419	0.08759	0.08589	2.75×10^{-7}
Q6	M	0.20413	0.20900	0.20657	5.65×10^{-7}
Q7	M	0.09128	0.09712	0.09420	8.12×10^{-7}
Q8	M	0.12983	0.13010	0.12997	1.74×10^{-9}
Q9	M	0.20037	0.16885	0.18461	2.37×10^{-5}
Q10	M	0.06834	0.06410	0.06622	4.28×10^{-7}
Q11	M	0.07497	0.06789	0.07143	1.19×10^{-6}
Q12	F	0.09261	0.08657	0.08959	8.69×10^{-7}
Q13	M	0.07927	0.07948	0.07938	1.05×10^{-9}
Q14	F	0.09510	0.09582	0.09546	1.23×10^{-8}
Q15	M	0.06012	0.05668	0.05840	2.82×10^{-7}
Q16	M	0.06012	0.05519	0.05766	5.79×10^{-7}
Q18	F	0.12307	0.11737	0.12022	7.74×10^{-7}
Q19	F	0.12113	0.14068	0.13091	9.10×10^{-6}
Q20	M	0.08792	0.08815	0.08804	1.26×10^{-9}
Q21	—	0.06621	0.06473	0.06547	5.22×10^{-8}
Q22	M	0.06276	0.06658	0.06467	3.47×10^{-7}
Q23	F	0.16139	0.17915	0.17027	7.51×10^{-6}
Q24	F	0.11132	0.11257	0.11195	3.72×10^{-8}
				sum =	0.00004672

[a] M = male; F = female.