Preliminary report on biological parameters for NA minke whales in Icelandic waters

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ABSTRACT

According to the IWC's stock definitions common minke whales (*Balaenoptera acutorostrata*) off Iceland belong to the Central North Atlantic stock or the Central stock. As a part of a special permit research program reviewed by the IWC Scientific Committee in 2003 a total of 200 minke whales were caught for scientific purposes during 2003-2007 (Víkingsson et al 2008). This study also included 88 animals from the Icelandic commercial whaling in 2006, 2008 and 2009. The sampling was distributed temporally and spatially in accordance with the relative distribution of common minke whales around Iceland. The overall sex ratio was 1.30/1 and 1.20/1 (female/male), for foetus and 0+ whales respectively, not significantly different from 1:1. New methods of aging minke whales was used after validation, the racemisation of aspartic acid from the whale's eye lens. The mean age for females and males were 18 and 21 years respectively, but the oldest female and male were 42 and 47 years respectively. Length at birth was estimated with the von Bertalanffy growth model as about 2 (95% CI 0 – 7) meters and females grew faster and attained lager size than males, asymptotic length was 8.17 (SE 0.24) and 8.42 (SE 0.12) meters for males and females respectively. Estimated age and length at sexual maturity was inconclusive for males and 6 (95% CI 0 – 7) years for females and 6.17 (95% CI 4.78 – 6.53) and 6.04 (95% CI 4.64 – 6.50) meters for males and females respectively. Pronounced seasonality was observed in testes weight, indicating a continuing testes development throughout the summer and autumn. Lack of data from the winter makes the exact timing of parturition and mating unknown. Ovulation and pregnancy rates were 87.7% and 74.5% in the sample, and 92.2% of mature females were reproducing. Mean time of conception was estimated to be in the middle of November and duration of gestation about 11 months. One minke whale female had twin foetus of total 79 females with foetus (1.3%).

Keywords: Growth, reproduction, minke whale, Balaenoptera acutorostrata*, Icelandic waters*

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INTRODUCTION

Minke whales in Icelandic waters belong to the subspecies *Balaenoptera acutorostrata acutorostrata,* which is one of the now three erected subspecies; *B. a. scammoni* in the North-Pacific, *B. a. a.* in the North-Atlantic and *B. a. without a name* in the Southern Oceans, and then since the end of the 19th century a relative species in the Southern Oceans *B. bonaerensis* (Reeves et al. 2002).

According to aerial and shipboard surveys conducted regularly since 1986 minke whale is Iceland's most numerous and widest spread baleen whale (Borchers et al. 2009; Pike et al. 2009a,b). Minke whales have been exploited in Icelandic waters since 1914 (Sigurjónsson 1982). This coastal based small-type whaling has mainly taken place inside the fjords and in the near shore waters within 30 nautical miles in W-, NW- and N-Iceland. In the period 1914-1936 the catch ranged from 1 to 37 animals, according to Sæmundsson (1931 and 1937) and from the late 1930's to 1960 the annual catches were below 100 animals (Sigurjónsson 1982). The average annual catches by Iceland for 1966-1970, 1971-1975, 1976-1980 and 1981-1985 were 105, 137, 198, and 188 animals respectively. According to Jonsgaard (1962) and Christensen (1975) in their analyses of the development of the Norwegian small-type whaling (these activities reached the Icelandic waters) the average Norwegian catch off Iceland in the period 1961-1972 was around 110 whales, but after the extension of the Icelandic fisheries jurisdiction the catches became insignificant. On average the Norwegian and Icelandic catches numbered around 200 minke whales in the years 1960-1985.

In 2003, The Marine Research Institute (MRI), in collaboration with a number of other Icelandic research institutions, submitted to the IWC, a programme for wide ranging research on cetaceans in Icelandic waters (Marine Research Institute 2003). The programme had multiple objectives and involved limited sampling of three species of whales in Icelandic waters under scientific permit. Specific dates for implementation were not set out in the proposal, although it was assumed that the sampling phase could be conducted in two years. In August 2003 the Government of Iceland decided to start implementation of the part of the programme concerning common minke whale. And in the year 2006 commercial whaling started again in Iceland, and since then Icelandic authorities have issued TAC for common minke whales and fin whales (*Balaenoptera physalus).*

Information on biology, including data on age and reproduction, were presented by Sigurjónsson (1982, 1988) which was based on material collected from the Icelandic coastal minke whale fishery in the years 1977-78 and by Sigurjónsson et al. (1990), which was based on material collected by whalers in cooperation with scientists of MRI, in the whaling seasons 1979 through 1985. The distribution of minke whales is more coastal than that of larger rorquals. Migrations in Icelandic waters are not well documented. It has been observed in Icelandic waters in all seasons and caught as late as in November some years, even though it seems most abundant off the coast of Iceland in the months May to September (Sigurjónsson and Víkingsson 1998). The distribution encompasses all Icelandic coastal waters, with high abundance spots in Faxaflói and off the Southeast-coast. Minke whales have been observed to be much more fish-feeders than the other larger rorquals, consuming considerable amounts of capelin (*Mallotus villosus*) and sand-eels (*Ammodytes sp.*) along with euphausids and larger bony fishes, in Icelandic waters (Sigurjónsson and Víkingsson 1998; Víkingsson and Elvarsson 2010). Available life-history data for minke whales in general implies that calves of minke whales are 2.5 – 2.8 meters and 150 – 300 kg, at parturition, length at maturity of females and males are 7 – 7.5 and 6.5 – 7 meters respectively. Maximum length (meters) and mean-weight (tones) are 10.7 and 7 and 9.8 and 5.7, for females and males respectively. Age at maturity is 5 – 7 years and 5 – 6 for females and males respectively, and maximum longevity for both sexes about 50 years (Víkingsson 2004).

Determining the age of minke whales has been of a problem, at least three organs have been studied in relation to aging, the *Tympanic bulla*, the ear plug and the eye lens. A method based on individual age readings needs to meet several criteria if it shall be applied for routine monitoring of harvested whale stocks. It needs to yield accurate assessment of age, which by other factors implies that a great degree of repeatability is needed, and for practical reasons it needs to be not too laborious. Sampling and processing of ear plugs from minke whales in Icelandic waters, particularly small whales, is both difficult and tedious. Age determination of minke whales by using ear plugs have also been shown to be rather complicated and they are very hard to get intact from animals in the minke whale catch in Icelandic waters (Sigurjónsson 1980) and not giving the same "good" results as for the fin whale (Lockyer et al. 1977) and sei whale (Lockyer 1976). On the other hand using the *Tympanic bulla* is easy, and the application in the field and the laboratory is far less time consuming than the reading of the ear plugs. However there were observed differences in the formation of the GLGs which does not make the GLGs in ear plugs and the bullas comparable. There was also observed a bad fit between bulla growth layers number and corpora counts in fin whales (*Balaenoptera physalus*) (Konradsson and Sigurjonsson 1989). Also (Sukhovskaya et al. 1985) found that bulla layers of Antarctic minke whales gave consistently lower counts than found in ear plugs from the same animals. (Larsen and Kapel 1982) reported difficulties in discriminating between primary and secondary growth layers, which affected the readability. New methods of aging minke whales was therefore put to the test, the racemisation of aspartic acid from the whale's eye lens, and after validating it was used for determining the age of the minke whales caught in the scientific whaling in Icelandic waters. The ages are presented and used in this paper, but for the methodology see (Audunsson unpublished).

The traditional way of determining the maturity stage of cetaceans is by analysis of the gonads. When an immature minke whale male reaches puberty and subsequently full sexual maturity, the testicle growth rate increases and the seminiferous tubules expand in diameter and become more elongated (Collet and Saint Girons 1984; Kasuya and Marsh 1984; Kinze 1990). The seminiferous tubules also take more space inside the testes tissues, their cover or density increases. The microscopic character and size of cetacean tubules indicate when the animals have reached sexual maturity, but definitions of sexual maturity based on histological examinations vary somewhat between authors. Some authors use three stages of maturity based on the appearance of the seminiferous tubules in the testicles: immature, pubertal and mature, like we do in this paper. Others have not felt this to be sufficient, suggesting a finer division of the pubertal stage, using the proportion of mature and immature tubules in the sample to indicate how far maturity has developed (Kasuya and Marsh 1984; Mitchell and Kozicki 1984).

Assessment of the maturity stage of females is generally easier, as each ovulation and pregnancy leaves a permanent scar in the ovary, the *Corpus albicans*. Based on the presence or absence of such scars, females are usually simply classified as either mature or immature, and pregnant if foetus was found in the uterus. Ovaries in many species of cetaceans do show an asymmetry in activity, meaning that one ovary (left or right) is more active than the other. This is often a species and age related characteristic. Some studies have been done on various reproductive parameters of the minke whale in North- and South-Atlantic and connected waters, but knowledge on their reproductive biology in Icelandic waters has been rather limited. In this paper we present our finding of biological parameters as growth and reproduction of minke whales, animals caught in the scientific whaling elucidated in the period of 2003-2007 and the commercial whaling in 2006, 2008 and 2009, and compare them with earlier data on the life history of the minke whale, in Icelandic waters, where such data was available, to investigate biological parameters trend over time, and add to the information about the population biology of the NA minke whale.

MATERIAL AND METHODS

Sampling and preservation

This paper encompasses the data collected during the scientific whaling in years 2003-2007 and commercial whaling in years 2006, 2008 and 2009. Sometimes when necessary we refer to older unpublished data. From whaling operations, either scientific or commercial, in the period 2003-2009, a total of 235 minke whales samples were collected from 288 animals, in the period 2003-2009, 128 females and 107 males. The sampling design of the special permit attempted to reflect seasonal and geographical distribution of the species in Icelandic waters (Table 1 and 2),.

The collection of material and field studies in the scientific programme was conducted, by the MRI whale scientists. The catch season normally lasted from late May through August/September, but a few whales were caught as early in the season as March and as late as November. Five vessels were operating in different coastal areas, and the collection of material depended on close cooperation with the whalers, which were therefore carefully instructed how to collect samples. The total sample of the study includes 288 minke whales thereof 200 from the research programme. 200 sex-organs and 116 eyes were collected (Table 3). Eyes were stored as soon as possible at -20°C. Ovaries and testicles were labeled, fixed and stored in 10% neutral formalin solution.

Measurements of length and weight

Minke whales were measured to the nearest 5 cm (some whales to the nearest feet) on-board or on the cutting-plane. In the scientific programme a standard morphometry was performed including several measurements of girth. For minke whale hunters it was customary to measure the length of the whales in feet[2], length in feet were consequently transformed to length in cm. Foetuses were measured to the nearest cm and weighed to the nearest kilo (kg) or to the nearest gram for the smallest ones.. Two minke whales were weighed straight for total weight. Due to this limited data on total weight, further analyses related to the whales' weights, for animals 0+ of age, was not possible.

Investigations on reproductive organs

During dissection of females, the uterus was carefully examined for the possible presence of a foetus, to see whether females were pregnant, and foetus collected if present. Mature females with foetus were classified as pregnant. In the laboratory sexual organs were weighed to the nearest gram (g), and their mean size used when pairs were obtained, or single weight used when the other was missing.

Ovaries

The ovaries were sliced at 0.5 cm intervals to study the numbers and sizes of corpora, in both ovaries and the ovarian bodies counted and measured. They were classified into *Corpora albicantia, Corpus luteum, Corpora atretica, Corpora abberantia*, follicles, white bodies, yellow bodies and other bodies, according to descriptions by Mackintosh and Wheller (1929), Laws (1961) and Gambell (1968) (Perrin and Donovan 1984). Length and breadth of each corpus was measured to the nearest mm, and the average of two such measurements was used as a measure of size of each corpus, except in case of the *Corpus luteum* which was measured in three dimensions, although not perpendicular on each other, and weighed on a scale. Each female was assessed mature or immature from the status of the ovaries. If a *Corpus luteum* or *Corpus albicans* were present in either of the ovaries, the whale was assumed mature,

[2] One foot equals 0.305 meters.

otherwise immature and pubertal females where characterized as having big and many follicles and developing ovaries.

Testes

Histology of tissues from testes was studied for sexual maturity. Both testes were weighed after removing the epididymis and a cross section taken from the mid-part along the longitudinal axis of one testis. After fixation samples about 1 cm in diameter were taken, one from the peripheral (P) or near surface part of the testes and one from the central part or core (C). The fixated samples were dehydrated, embedded in paraffin, sectioned on a microtone in 6-10 µm slices, mounted on a glass and stained with Delafield's haematoxylin and counter stained with eosin (H & E). The stained sections were examined under a microscope equipped with an ocular micrometer and magnification up to 400X, after being mounted on a glass. Ten tubules were randomly chosen for measurement of diameter. All measurements were made from the basement membrane or seminiferous epithelium if basement membrane was detached from the seminiferous epithelium. The mean size of the tubules in the sample was calculated from all measurements. Each sample was assessed to 1 - 3 stages of sexual maturity from the appearance of the tubules and surrounding tissue: immature, pubertal and mature (Table 4). The primary criteria were the relative size and appearance of the tubules and interstitial tissue (Mitchell and Kozicki 1984; Harrison 1969; Mackintos and Wheeler 1929), where the diameter of the testis tubules and size of the cells were determining factors. When two samples were available from the same testis (P and C), the final maturity stage of the animal was determined using a combination assessment (Table 5) (Sigurjónsson et al. 1990; Halldórsson and Vikingsson 2001).

Estimation of tubules density or cover was made by counting tubules in cross-sections using 10×10 ocular grid planimeter in the microscope. Specimens were placed randomly under the microscope and tubules counted which touched the crosses. Counts were mostly done under 4x10 magnifications, but sometimes when the sample was in bad condition 10x10 magnification was needed, and were never made in the area of the major arteries of the testis. Each sample was counted at two positions central and peripheral in the testes' tissue and the mean value estimated, by adding the values together and dividing by two.

Age determination

Ages were determined with the method of racemisation of aspartic acid (ASP) from the whale's eye lens; see (MRI 2003). ASP-ages, which were decimal ages, were compared with total number of corpuses (*Corpus albicans, Corpus luteum* and *Corpus atretica*) in mature females, because from ovarian corpora numbers and transition phase age, the age of mature females have been deducted (Ohsumi 1986).

Estimation of parameters of growth in length

For estimation asymptotic length (Y_∞), growth constant (K) and theoretical age at zero length (t_0), for male and female minke whales, three growth-curve models were tried out;

Equation 1. Logistic $[y = Y_\infty(1+e^{-K(t-t0)})^{-1}]$,

Equation 2. Richard's $[y = Y_\infty(1-e^{-K(t-t0)})^{m}]$,

Equation 3. von Bertalanffy $[y = Y_\infty(1-e^{-K(t-t0)})]$,

Akaine Information Criteria (AIC) was used to decide which model fitted the growth data the best.

Statistical analyses

Sex-ratio was studied using chi-squared, assuming equal proportions of females and males, foetus and 0+ animals. Mean body length and age of reaching maturity (just two groups mature or non-mature, immature and pubertal animals were classified as non-mature other groups as mature) was estimated for females and males using Logistic Regression, $\text{logit}(\pi_i) = \alpha_i + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots \beta_q x_q$, incorporating Julian day, months and years of sampling to see if those time terms had influence on the results, in case of the age were also length, and length and age interactions included. Three non-linear models were fitted to the age and length data, the Logistic, Richard's and von Bertalanffy´s growth curves.

Mean diameter of ovarian bodies were compared with ANOVA. Diameter of follicles, as well as maximum size of *Corpus albicans*, *Corpora lutea* and *Corpora albicantia,* were regressed against Julian day, month and years of sampling, using a simple linear model. A Nonlinear Logarithmic Model was fitted to data on the diameter of *Corpus albicans* and total number of *Corpus albicans*. The relationship between corpora number and ASP-age was investigated by using least trimmed squares and resistant regressions, as well as an ordinary linear model. Mean diameter of seminiferous tubules in testes were compared with ANOVA and increases per unity were determined with General Linear Modeling. Multiple comparisons were made with the method of Tukey honest significant differences. Correlation between weight of testes and the mean diameter of the tubules was investigated with Spearman Rank correlation coefficient. The relationship between weight of testes and the mean diameter of seminiferous tubules as well as the relationship between mean-diameter and weight of *Corpus luteum,* and day of the year and foetus growth in weight was tested with *ln-ln* transformations using a Linear Model (a power relationship assumed). Weight of testes in relation to ASP-age was smoothed with LOESS for creating a trend line. Length and weight relationship, and length and day of the year relationship of foetuses, were determined with Non Linear Modeling. Statistical analyses were performed with R (open-source software), see R's home-page at http://www.r-project.org (Verzani 2005; Everitt and Hothorn 2010).

RESULTS

Length, weight, twin foetuses and sex ratio of minke whales

Most of the caught minke whales where mature animals (Table 2.), for 45. Female were significantly longer than male foetuses, on average, taken into account day of the year and sampling year ($F_{1,70}$ = 13.04, p = 0.01). Average total length for foetus females and males being 106,0 and 90,7 cm respectively. The mean length of foetuses with unknown sex was 53,1 cm. Average length for 0+ females and males in the sample were 769.8 and 744.4 cm respectively. A 732 cm long pregnant female (D0601), 11 years of ASP-age, caught 21 July 2006, weighed 3405 kg and a 740 cm long mature male (D0603), 16 years of ASP-age, caught 22 July 2006, weighed 3682 kg. Total sex ratio was 128 female and 107 males, for 0+ animals, not significantly different from 50/50 (Chi square = 1.88, df = 1, p = 0.17). Foetal sex ratio was 27 females and 35 males, not significantly different from 50/50 either (Chi square = 1.03, df = 1, p = 0.31). One out of 79 females had twin foetus (1.3%). The female was 8.70 meters in length and 42 years of age, caught 3 July 2006, which had a 34 cm male and 32 cm long female foetus, in her womb.

Length and weight relationships

Foetus

A nonlinear power relationship was fitted to the available data on length and weight of foetuses, for combined sexes (Figure 1).

$$W = 3.682 \times 10^{-5}(\text{SE } 3.799 \times 10^{-5}) * L^{2.758(\text{SE } 0.206)}$$

(RSE=4.095 and df = 33). The power was significantly different fro zero (T-value = 12.39, p < 0.001), but the intercept was not.

Ovaries

Weight and mean-diameter of *Corpus luteum* from female minke whales, showed a power-curve relationship, logarithmic fit gave a straight line with intercept = -6.094 (SE 0.616) and slope 2.621 (SE 0.155) (Figure 2). The intercept and slope were both significantly different from zero, T-value = -9.89, p < 0.001 and T-value = 16.90, p < 0.001 respectively (RSE=0.161 and df = 43, $r^2 = 0.87$, $F_{1,43} = 285.50$, p < 0.001).

Testes

There was a significant correlation between weight of testes and the mean diameter (D_{semtub}) of the tubules ($r_s = 0.84$, df = 5, p < 0.01) for mature males. The relationship was best described by a power function (*ln-ln* relationship). Scatter of the data was high and the relationship for mature males was estimated as;

$$Ln(W_{test}) = 0.790(SE\ 1.525) + 1.139(SE\ 0.301)\ ln(D_{semtub})$$

($R^2 = 0.37$, $F_{1,24} = 14.32$). The slope was significantly different from zero (p = 0.001), but not the intercept (Figure 3).

Growth

Foetus

Significant difference in length of foetuses (L_f) were observed, in relation to natural logarithms of days of the year (*ln*D) and sex (three factors sex unknown, males and females, sex unknown being the reference point), T-value and p were respectively 8.42 p < 0.001, 25.90 p = 0.01, 37.11 p < 0.001. Due to many foetuses with unknown sex, especially at low length and weight, all foetuses were combined and length only studied in relation to Julian Day, showing a curve linear relationship with day.

$$L_f = 0.002(SE\ 0.003)\times D^{2.022(SE\ 0.242)}$$

(RSE = 29.76, df = 70 and AIC = 696.91), increasing from about 30 cm in total length in April to about 1.57 meter in September (Figure 4).

Natural logarithms of foetus weight (lnF_w) increased significantly with natural logarithms of day (*ln*D) (T-value = 4.79 p <0.001) and females and males foetus weighed significantly more than foetus of unknown sex (T-value = 3.12 p= 0.004 and T-value = 2.30 p = 0.03), but not with years of sampling. A curve linear relationship could not be fitted, however the linear *ln-ln* relationship;

$$Ln(F_w) = -23.486\ (SE\ 6.027) + 4.783(SE\ 1.130)ln(D),$$

described this significantly ($R_{ad}^2 = 0.36$, $F_{1,29} = 17.91$, p <0.001), both intercept and slope were significant (T-values and p were -5.65 p <0.001 and 6.02 p < 0.001 respectively), implying that a power curve-linear relationship existed.

According to the established length-weight relationship of foetus (Figure 1) a 30 cm and 157 cm long foetus would have body weight of 0.4 and 82 kg, growing in weight nearly 82 kg in 6 months.

0+ animals

Parameters for growth curves are presented in Table 6. Of the growth models tested von Bertalanffy gave the lowest AIC-values, both for females and males (Figures 5 and 6). The Logistic growth model did nearly as well as the von Bertalanffy model and the Richard's growth model, which has four parameters to fit, did well for the female data; however it was not possible to fit the male data to it. Asymptotic length, growth constant and the time constant (t_0), theoretical age of zero length for females and males, estimated with the von Bertalanffy growth model, were 8.42 and 8.17 meters, 0.16 and 0.08 cm/year, and -1.61 and -13.89 respectively. Using the female von Bertalanffy growth-model to calculate length at age zero (calf length at birth), gave 1.9 ((negative values judged unrealistic) – 2.9) meters (Figure 5).

For females, the mean length and age of immature, pubertal, mature, and pregnant animals were 6.51 and 8.5, 7.60 and 10.2, 7.73 and 18.7, and 7.98 meters and 19.7 years, respectively. For males the respective information on length and age was, 5.75 and 11.6, 7.16 and 21.4, and 7.57 meters and 21.4 years for immature, pubertal and mature animals respectively (Table 7). One male (B0301) separated oneself markedly from other males being 13 years of age, but only 5.2 meters in length (the lowest point on Figure 6).

Foetuses, ovaries, weight and number of ovarian bodies

The single mean weight of ovaries varied from immature to pregnant minke whale females, being of lowest weight in immature females, however of similar weight in pubertal, mature and pregnant females (Figure 7). The sexual maturity of 104 females of 123 could be determined by the presence of one or more corpus in either of the ovaries, revealing 84.6% of the sample sexually mature and 15.4% immature (Table 2). The frequency distribution of the total numbers of *Corpus luteum*, *Corpora atretica* and *Corpora albicantia* in both ovaries is shown in Figure 8. Total of 33 (57.9 % of the sample) mature females with both ovaries collected had less then 10 corpora of this type, whereas 7 (12.3%) animals had in excess of 20. The larges number of such corpora in a pair of ovaries was 45.

In the total sample 47 animals which had active *Corpus luteum*, i.e. *Corpus luteum* of pregnancy or ovulation, 63.8 % (30) had foetus recorded. Foetus was found in all 30 of 47 females with *Corpus luteum*. Four sexually "matured" females had only *Corpus albicantia* in the ovaries (A0406, A06101, C0609 and C0613), i.e. was neither pregnant nor ovulating, so about 92 % of mature females were reproducing. A total of 79 females had foetus and one female (1.3%) twin foetus.

Length at maturity

Females

Results from the GLM analyses indicated that Julian Day and year of sampling did not influence the onset of maturity of females , however length of females did influence that significantly ($z = 3.82$, $p < 0.001$). The model being;

$$\text{Logit}(\pi_i) = -6.893(\text{SE } 2.186) + 0.011(\text{SE } 0.003)$$

(Residual Deviance = 91.43, df = 121, AIC = 95.43), which indicated that the total length at which 50% of females was mature was equal to 603.8 cm (95% CI 463.8 – 649.6). The longest immature female was 7.6, the shortest mature female was 5.0 and the shortest mature and pregnant female was 6.8 meters (Table 7).

Males

Results from the GLM analyses indicated that Julian Day and year of sampling did not influence on the onset of sexual maturity, however length of males did influence that significantly ($z = 3.20$, $p = 0.001$). The model being;

$\text{Logit}(\pi_i) = -10.049(\text{SE } 3.456) + 0.016(\text{SE } 0.005)$

(Residual Deviance = 58.31, df = 84, AIC = 62.31), which indicated that the total length at which 50% of males was mature was equal to 616.7 cm (95% CI 478.1 – 652.6). The length range for pubertal males was 6.0 – 8.4 and the shortest mature male was 5.7 meters (Table 7).

Age of maturity

Females

Age at maturity was estimated with a logistic regression as being at 6 years of age (95% CI (negative values omitted) – 7 years). The fit was just significant for age ($p = 0.04$). The intercept was not significant. Calculating smoothed percentage mature from the coefficients of the logistic regression gave too high values in the lower age-ranges, but more realistic ones in the older ages (Table 8). Results from an ordinary linear regression of ASP-age and total number of ovarian corpuses, indicate that age of maturity was 8.8 (SE 0.70) and that each year 0.96 (SE 0.06) corpuses were formed, that is to say 1.04 years between corpus formation. Both intercept and slope was significantly different form zero ($p < 0.001$). Results from least trimmed square regression on ASP-age and total number of ovarian corpuses (*Corpus luteum, Corpora atretica and Corpora albicantia*), indicate that females become mature 10.1 years old and after that produce 0.77 corpuses annually, or there were 1.30 years between ovulations. The result of resistant regression indicate that females became mature 8.8 years old (SE = 0.65) or on the 95% confidence interval 7.5 – 10.3 years, and produce 0.99 (SE = 0.054) corpus annually, or there was just about 1 year between ovulations (Figure 9). The youngest mature female caught was 7 years of age and the only one pubertal female caught was 10 years of age (Table 7).

Males

Age at maturity could not be estimated with a logistic regression of age on whether mature or not, as there was not a significant fit. Even so the coefficients from the logistic regression were used to calculate %-mature in each age-class, giving to high values for the younger ages, but more realistic values for the older ages (Table 8). The youngest mature male was 6 years of age and the youngest of the seven pubertal males caught was 8 years of age (Table 7). Mean weight of single testes (the average weight of the testes par or just the one testis sampled) was the highest in mature males, much lower in pubertal and immature males. Testes weight was not found to be significantly different in relation to years of sampling, day of the year and length of animals. Their mean weight was much higher in mature males than in pubertal and immature males 744.25, 167.50 and 35.33 respectively (Figure 10).

Maximum weight of single testes in immature, pubertal and mature males was 67, 260 and 1362 g respectively. Minimum weight of single testes in mature males was 337 g (Figure 11). Males with immature testes were less than 13 years old. Males with pubertal testes weight were 8, 13 and 38 years (this 38 years old male probably was an outlier). The youngest males with mature testes weight were, 10 years. Males of age 20 – 30 years were observed to have the testes with the highest weight.

Seasonality of reproduction

Females

Diameter of ovarian bodies was significantly different between types of bodies and maturity stages of females ($p < 0.001$ in all cases). Corpora were significantly largest in pregnant females and follicles smallest in immature females in general ($p < 0.001$). Only one pubertal female was found in the sample of females (Figure 12), which can cause problems in the ANOVA. Further investigation showed for pregnant females that neither Follicle diameter nor *Corpus luteum* diameter showed significant trend with Julian day, month and/or year (Figure

13). However *Corpora albicantias'* diameter did decrease with sampling year. On the other hand diameters of the maximum size *Corpus albicans* was not significantly different between days of the year or sampling years (Figure 14).

There were no relationship between foetus weight and diameters of *Corpora lutea*. However diameter of *Corpora albicantia* (D_{ca}) declined with total number of *Corpus albicans* (N_{ca}), following a logarithmic relationship, where;

$$D_{ca} = 15.151(0.932) - 1.743(0.439)\times ln(N_{ca})$$

Both intercept and slope were significantly different from zero ($p < 0.001$) (Figure 15). Underlining the fact that *Corpora albicantia* does not disappear, instead reach a minimum size about 10 mm, and form a permanent scar in the ovaries.

Males

Diameter of seminiferous tubules in testes

Seminiferous tubule diameter in testes were significantly different in size, in location (PC, P and C) and in the three maturity stages (immature, pubertal and mature), $F_{4,1584} = 91.85$ and $p < 0.001$ (Table 9). Seminiferous tubules were on average with smaller diameter in immature and pubertal than mature minke whale males. Peripheral seminiferous tubule had smaller diameter than tubule from the core in general, on average 0.011 mm less. These differences all had high significance ($p < 0.0013$), but there was observed a significant interaction between diameters and animals.

Results from GLM indicated that diameter of seminiferous tubules varied significantly with day of the year (T-value = 5.21, $p < 0.001$). Increased linearly from May to September, being on average 1.17, 1.27, 1.37, 1.47 and 1.56 mm, in May, June, July, August and September respectively, an average increase about 0.13 (SE = 0.03) mm each month. There was also a significant difference in mean tubule diameter after length of animals (T-value = 4.49, $p < 0.001$). The mean tubule diameter was also significantly different between maturity stages in the way that mature males had significantly wider tubule than immature (T-value = 3.79, $p < 0.001$), but pubertal not. Mean seminiferous tubules diameter being 1.26, 1.35 and 1.43, for immature, pubertal and mature, respectively. In Figure 16 the mean diameter of the seminiferous tubules was related to days of the year for the three maturity stages. There was a significant increase in tubules diameter with days 0.44 (SE 0.08) per day and this daily increase was significantly different between immature, pubertal and mature whales, as mentioned before. The tubules in the testes of immature animals increased not at all, but the increase was significantly higher in the mature than in the immature whales.

The relationship between the mean diameter of seminiferous tubule (D_{semtub}) and weight (W_{test}) of testes was a power curve (RSE = 0.79, $R^2 = 0.87$, $F_{1,4} = 27.45$, $p = 0.01$) (Figure 3).

$$Ln(W_{test}) = 1.826(SE\ 0.787) + 0.878(SE\ 0.168)\times ln(D_{semtub})$$

The slope was significantly different from zero ($p = 0.01$), but the intercept not.

Density (or cover) of seminiferous tubules in testes

There was observed a highly significant correlation (Sperman rank = 0.40, df =81, $p < 0.001$) between diameter of tubules and the mean density (or cover) of combined cover measurements in peripheral and central parts of the testes (Table 10). The difference between cover of tubules in central and peripheral samples were significant ($F_{2,74} = 5.56$, $p = 0.01$). Tukey multiple comparison of means indicated that there was a significant difference between cover of tubules in peripheral and central parts of testes between pubertal and immature males (p = 0.04) and between mature and immature males (p = 0.01), but not between mature and pubertal males.

There were not significant differences in combined cover, between maturity stages of males and not significant trend with years of sampling. However there were observed a significant positive trend between cover and Julian day (p = 0.02). Estimated increase was 0.1% (SE = 0.04) per day (Figure 17).

DISCUSSION

Sampling and whaling operations

Sample from the early spring and winter was lacking, and also sample of small and young minke whales. Consequently, one must be continually aware of the possibilities of bias, due to the nonrandom nature of the collection of such samples. There is evidence for changes in school size of minke whales and sex and age-groups composition with both latitude and time, but most noticeably over the period of greatest sexual activity. The males do not stay with females over a protracted period, and the pregnant females quickly disappear from the wintering grounds –not really known were they are. The sample presented here is derived only from the summer feeding grounds off Iceland and is therefore not necessarily representative of a breeding population. Mating occurs predominantly in the winter months, although ovulation can occur throughout the year. The breeding grounds off Iceland are unknown, although satellite tracking has indicated a link to western African waters. Lactating females with calf are a rare sight in Icelandic waters indicating that most calves are weaned before entering the Icelandic feeding grounds in spring..

Age determination

Age determination of minke whales by using ear plugs and *Tymphanic bulla*, have been shown to be rather complicated (J. Sigurjónsson 1980) and not giving as good results as for the fin whale (Lockyer et al. 1977) and sei whale (Lockyer 1974).

Making assumption on age at sexual maturity and ovulation rate, age-determination (A) of mature females can be derived from the formula;

Equation 4. $A = 7(4\text{-}10) + 1.4(1.1\text{-}1.9)\times O$ (Ohsumi 1986)

where O was the sum of numbers of *Corpora albicantia*, *Corpora lutea* and *Corpora atretica*, in the combined left and right ovaries, similar equation has been used by Japanese whale researchers (Lockyer 1972). It can not be used to age immature females and males, so another method based on racemisation in aspartic acid in lens tissue of the eye for determining age, was used for all animals (Bada et al. 1980). After thorough calibration with available age data from all ages of minke whales, from foetus to old whales, ages of caught minke whales were determined with this ASP-age method based on racemisation in aspartic acid in lens tissue of the eye; see MRI (2003).

Horwood (1990) presents the annual ovulation rate as 1.0 to 1.1, using corpora and bulla ages and corpora and ear plug ages, which was the same as observed in this study using corpora and ASP-ages.

Female reproduction

In the present study about 85.0% of the mature females were determined pregnant and that 92.2% mature females were reproductively active. In (Jóhann Sigurjónsson et al. 1990) about 80% mature females were pregnant and in a special sample thoroughly investigated 93.8% were pregnant. This was similar as observed in the Barents Sea and off N-Norway, 95.5% (Jonsgaard 1951), Barents Sea, E and W Greenland 94.4%, 100% and 89.9% respectively (Christensen 1981 and 1974), and W-Greenland 89% (Larsen 1984). This lower %-pregnant value in this study can be caused by loss of foetus from the cows, at the shipside on the way to harbors.

Logistic regression results indicated that the total length at which 50% of females was mature was equal to 603.8 cm (95% CI 463.8 – 649.6), which was lower than Stenseth et al (1993) observed for the minke whale females in the Barents- and Norwegian Sea, being 7.2 meters. The extremely low sample size in the present study, particularly for the lower age classes must however be born in mind. The longest immature female was 7.6, the shortest mature female was 5.0 and the shortest pregnant female was 6.8 meters, were closer to that value. (Jóhann Sigurjónsson et al. 1990) observed 7-7.5 m total length as the size female minke whales in Icelandic waters attained sexual maturity (L_m) and suggested that this size conformed well to other earlier data on L_m from other areas, e.g. from Norwegian waters 24 and 23.5 feet (Jonsgaard 1951; Christensen 1981) respectively, and the 750 cm off W-Greenland and 737 cm from Newfoundland material (Larsen 1984; Mitchell and Kozicki 1975). Age-at-maturity of 6 years was, however the same or similar as Stenseth et al. (1993) reported for the minke whale females in the Barents- and Norwegian Sea, and Horwood (1990) presents in table 7.1. The regressions of ASP-age with total number of corpora gave age at maturity about 9 years (8 – 10).

One female out of 79 (1.3%) had twin foetus, that was higher than the 0.6% multiples reported by Horwood (1990). It was generally considered by whale experts that even twins were unlikely to go to term. No sure twins have been observed free-living in the oceans Horwood (1990)?

Male reproduction

Generally, variation in testes weight at attainment of sexual maturity is a problem when considering the use of this as criteria for maturity in mammals. The present results show, however, a clear gradient of tubule size and particularly in densities of tubules, which we consider the most convenient means of determining the sexual status of the animals (Table 4).

Logistic regression results indicated that the total length at which 50% of males was mature was equal to 616.7 cm (95% CI 478.1 – 652.6), which was a little shorter than the 675 cm reported by Stenseth et al. (1993), for the minke whale males from the Barents- and Norwegian Sea, however, overlapping the values Horwood (1990) gives in table 7.1, for males, in his monograph about the biology and exploitation of the minke whale. The length range for pubertal males was 6.0 – 8.4 and the shortest mature male was 5.7 meters. However the L_m for male minke whales (Sigurjónsson et al. 1990) observed for animals in the catch of the seasons in 1977 through 1985 was somewhat higher, 7.1 meters, than observed by (Jonsgaard 1951; Christensen 1981), but mentions that criteria for maturity was somewhat different.

Using weight of testes as criteria for maturity (Figure 11) indicates, that all immature males were less than 13 years of age, pubertal males were 8-13 (with one 38 years of age as an outlier), and the youngest mature males of age 10-15. Using other criteria indicates. that age-at-maturity for minke whale males in Icelandic waters could be on the interval 6 - 8 years (Table 7), or similar as reported by Stenseth et al. (1993), for the minke whale males from the Barents- and Norwegian Sea. The weight of testes reached a maximum just after the 20th year-at-age for males, which was hardly significant due to fewer samples in the older age-classes. Or, if real, an interesting observation, which was hard to explain, however here age-specific migration differences could play a part and of course some effects of the sampling methods.

Calculating male %-maturity by smoothing, using the coefficients of the non-significant logistic regression of mature or non-mature on the male age, gave to high values for the younger males, but more realistic values for the older males, indicating that males older than

15 years were about 85% mature and older males close to 90% with 95% as a maximum (Table 8).

Growth, asymptotic length and other factors of morphological importance, comparison of the Icelandic minke whale with other minke whale populations in the world seas

The value of the power constant (2.8) in the length and weight relationship of foetus was quite comparable to those observed in earlier investigations, inside the interval 2.7 - 2.9, but the intercept was different about 100 times smaller (Horwood 1990). The slope of a curve linear relationship for growth in foetus in length was quite similar to those presented in (Horwood 1990) also, even those use months as time frame, not days. A curve linear relationship for the growth of foetus in weight could not be established due to too few and variable observations. The *ln-ln* linear model implies that the relationship was a power-curve with a slope 4.77, which would indicate a weight about 165 kg at birth, using the length-weight relationship for foetus presented in this paper. Gompert's growth curve, which fits the growth of seal foetus reasonably well (Yunker et al. 2005), would probably be a better chose if the data would have made it possible to fit that model. Víkingsson (2004) estimated that calves of minke whales were 2.5 – 2.8 meters and 150 – 300 kg at parturition. .

Jonsgaard (1951) considered the maximum average length 8.2 m for males and 8.8 m for females, which was more similar to the values from Icelandic waters. Maximum lengths observed were 9.0 and 8.7 meters for females and males respectively (Table 7). (Christensen 1981), which aged minke whales using growth layers in the *Tympanic bulla*, fitted the von Bertalanffy growth equation to the Norwegian minke whales and reported L_∞ = 8.33 and 9.07 m, K = 0.169 and 0.142 per year, and t_0 = -4.3 and -4.3 for males and females respectively. Somewhat higher values than presented here for the Icelandic minke whales, but more similar after the modifications Christensen made by drawing by eye, figures 4.3 on page 74 in Horwood (1990). Mitchell and Kozicki (1975) fitted a von Bertalanffy growth curve, to Newfoundland minke whales, to find for females L_∞ = 7.6 m, K = 0.25 per year, and t_0 = -3.2 years. Shorter asymptotic length, but similar K and t_0 as for the Icelandic waters minke wale females, probably because of a lack of older females in the Newfoundland sample (Horwood 1990). From catches off Japan, Omura and Sakiura (1956) reported maximum length of 8.5 m for females and 7.9 for males. Maximum longevity for both sexes have been found to be about 50 years (Víkingsson 2004), and the oldest females and males observed here were 42 and 47 years of age (Table 7).

Onset of maturity and the transition phase

Aging of minke whales were not based on reading GLG's from ear-plugs or *Tymphanic bullaes* see (Lockyer 1972; Purves 1960), so no transitional phase was available. Earlier studies e.g. (Sigurjónsson 1980) questions the validity of using ear-plugs in ageing of minke whales in North-Atlantic waters. Reading GLGs in the *Tymphanic bulla* has neither given satisfactory results. Newer data, based on the racemisation of aspartic acid from the whale's eye lens, indicate that Icelandic minke whales females reach maturity at the age of 8-10 year. Moreover calculations based on ASP-age indicate that 10, 15, 20 and 25 years old females were 74, 89, 95 and 98 %-mature, respectively (Table 8).

Temporal changes in reproduction

The female reproductive data did not show any seasonal differences in values, except the foetus grew of course. The intercept of the foetus length growth-curve indicated that zero length was at day one of the year. Taking t_0 into account and putting it at 43 days (Horwood 1990), would indicate that mean day of conception was in the middle of November, the year before. Likewise, foetus reaches birth-length (290 cm) in day 360, indicating that mean time of birth was in late December and duration of gestation about 11 months, or similar as presented by Horwood (1990). The great variability around the linear growth-curve of foetus length and weight was tempting to explain with great variability in dates of conception, rather than sampling error.

The increase in the mean diameter and density of seminiferous tubules in male testes' indicates that reproductive activity was increasing from May to September. In minke whale males stationed in Icelandic waters, there was no indication of a peak in reproductive activity in the time period of the study. This fits to the life history of the NA minke whale, with a peak reproductive activity of males occurring in February each year, at time of breeding (Gísli A Víkingsson 2004).

Biological parameters and their trends over time

The fin whale, the minke whale close relative shows some marked trends in biological parameters over time (Lockyer and Sigurjónsson 1992). Sigurjónsson (unpublished) and Sigurjónsson et al. (1990) present biological data on the Icelandic minke whale from the period 1977 – 1978 and 1979 – 1985, respectively. Different ageing method was used in these older studies than this newer one, so age-related parameters can not be compared; however length related biological parameters should be comparable.

In the period 1977 – 1978 Sigurjónsson estimated length at 50% maturity as 24.4 (7.44 meters) and 22.4 (6.83 meters) feet and in the period 1979 – 1985 Sigurjónssons et. al (1990) as 7 – 7.5 and 7.1 (SD 0.671; N 72) meters for females and males respectively, somewhat higher than obtained in this study, 6.04 (95% CI 4.64 – 6.50) and 6.17 (95% CI 4.78 – 6.53) meters for females and males respectively.

In Sigurjónsson et. al (1990) study 80% of mature females were determined pregnant, which was similar to the value from present study, 74.5%.

Unfortunately, it was impossible to tell whether these are real differences in length of onset of maturity and % of mature female pregnant, or artifacts due to the many methodological problems of sampling and estimation of parameter values, from three different studies.

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TABLES

Table 1. Number of minke whales (*Balaenoptera acutorostrata*) sampled by months, in the scientific whaling program and in the commercial whaling in Icelandic waters, in the period 2003-2009

Month	Females	Males	Total
April	3	0	3
May	7	3	10
June	38	21	59
July	37	20	57
August	27	30	57
September	10	10	20
October	1	0	1
Not known	5	23	28
Total	128	107	235

Table 2. Reproductive status of minke whales (*Balaenoptera acutorostrata*) caught in the special permit program and commercial whaling in Icelandic waters, in 2003-2009

		Females (n)	Males (n)
Immature		11.32% (12)	4.76% (4)
Pubertal		0.94% (1)	14.28% (12)
Mature		87.74% (93)	80.95% (68)
	Pregnant	74.53% (79)	
Total		100.00% (106)	100.00% (84)

Table 3. Biological material from minke whales (*Balaenoptera acutorostrata*) caught off Iceland, in the period 2003-2009

	Sex organs			
Year	**Testis**	**Ovaries**	**Eyes pairs from animals (aged)**	**Foetus**
2003	**22**	**13**	**25**	**5**
2004	**11**	**15**	**25**	**2**
2005	**16**	**14**	**28**	**1**
2006	**29**	**28**	**56**	**13**
2007	**9**	**25**	**31**	**7**
2008	**0**	**6**	**0**	**0**
2009	**1**	**11**	**1**	**2**
Total	**88**	**112**	**166**[3]	**30**

[3] Eye lenses from total of 18 animals were unusable for aspartic acid racemisation chemical analyses, making total collected eyes 184.

Table 4. Maturity stages of testes, by description, in male minke whales (*Balaenoptera acutorostrata*)

Stage	Description
Immature	Very small tubules, few large cells with dark stained large nuclei filling the tubular lumen
Maturing	Both immature and mature tubules can be found in the samples. Only few cells of either types could be found in some cases
Mature	Large tubules having large cells with light stained nuclei, mostly near the edge of the tubules. The lumen of mature testis was never completely filled with cells, even in well preserved samples
Actively mature	Males judged as mature are not necessarily in active state. Active spermatozoa production has, however, not been noticed and no attempt was made to classify males by searching for spermatozoa

Table 5. Assessment of maturity status of male minke whales (*Balaenoptera acutorostrata*) based on combinations of maturity assessments of peripheral (P) and central (C) testis tissue samples (final classification)

	Maturity of sample C		
Maturity of sample P	Immature	Pubertal	Mature
Immature	1 (immature)	1 (pubertal)	1 (pubertal)
Pubertal	0 (immature)	1 (pubertal)	9 (mature)
Mature	0 (pubertal)	0 (pubertal)	71 (mature)

Table 6. Parameters of the growth curves, for minke whales (*Balaenoptera acutorostrata*), in Icelandic waters. The model with the lowest AIC value fits the best

Growth curve model	Asymptotic length (L_∞)	Growth constant (K)	Theoretical age of zero length (t_0)	Fourth fitting parameter in the model (m)	Akaike Information Criteria (AIC)
Von Bertalanffy's	Females 842.2 (12.304)*** Males 817.1 (24.212)***	Females 0.160 (0.023)*** Males 0.076 (0.027)**	Females -1.61 $(1.146)^{ns}$ Males -13.89 $(7.089)^{ns}$	None	Females 892.67 Males 862.93
Logistic	Females 835.5 (10.810)*** Males 813.9 (21.950)***	Females 0.211 (0.029)*** Males 0.088 (0.029)**	Females 1.85 (0.826)* Males -8.88 $(5.008)^{ns}$	None	Females 893.07 Males 863.44
Richard's	Females 841.8 (16.239)*** Males (no fit)	Females 0.1624 (0.068)* Males (no fit)	Females -1.96 $(11.204)^{ns}$ Males (no fit)	Females 1.092 $(2.984)^{ns}$ Males (no fit)	Females 894.67 Males (no fit)

Table 7. Comparison of mean length, mean age and ranges of immature, pubertal and mature male and female minke whale (*Balaenoptera acutorostrata*), with information about pregnancy of females, from the whaling in 2003-2009

	Females											
	Immature			Pubertal			Mature and not pregnant			Mature and pregnant		
	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range
Age (yr)	8.5	12	3.4 – 14.5	10.2	1	10.2	18.7	7	6.7 – 29.7	19.7	54	10.0 -41.7
Length (cm)	650.58	12	461 - 762	760	1	760	772.91	11	502 – 872	797.99	78	682 - 900

	Males								
	Immature			Pubertal			Mature		
	Mean	N	Range	Mean	N	Range	Mean	N	Range
Age (yr)	11.6	3	7.2 – 14.3	21.4	7	8.1 – 46.8	21.4	71	6.1 – 47.4
Length (cm)	575.25	4	508 – 706	715.78	9	603 - 836	756.86	74	566 - 870

Table 8. Proportion of mature minke whales (*Balaenoptera acutorostrata*) in relation to ASP-age, in Icelandic waters, in the period 2003-2009. Smoothed(%) is estimated %-mature for ages with the values of coefficients from the logistic regression

Females																									
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25+
Mature	-	-	0	-	1	1	2	2	0	2	10	2	4	5	3	4	5	2	2	2	3	1	3	5	13
Immature	-	-	1	-	0	0	1	1	2	2	2	1	0	0	0	0	1	0	0	0	0	0	0	0	1
N	0	0	1	0	1	1	3	3	2	4	12	3	4	5	3	4	6	2	2	2	3	1	3	5	14
%-Mature	-	-	0	-	100	100	67	67	0	50	83	67	100	100	100	100	83	100	100	100	100	100	100	100	93
Smoothed(%)	-	-	41	-	51	56	61	66	70	74	78	81	84	86	89	90	92	93	94	95	96	97	97	98	98
Males																									
Mature	-	-	-	-	-	1	2	0	2	4	1	1	1	0	4	5	6	5	2	-	4	5	1	2	24
Immature	-	-	-	-	-	0	1	1	0	0	1	0	2	1	0	1	1	0	0	-	0	0	0	0	2
N	0	0	0	0	0	1	3	1	2	4	2	1	3	1	4	6	7	5	2	0	4	5	1	2	26
%-Mature	-	-	-	-	-	100	67	0	100	100	50	100	33	0	100	83	86	100	100	-	100	100	100	100	92
Smoothed(%)	-	-	-	-	-	64	67	69	72	74	77	79	81	83	84	86	87	89	90	-	92	93	94	94	95

Table 9. Summary statistics, for seminiferous tubule diameter (mm) grouped by sample location (PC = combined peripheral and central, P = peripheral, C = central) and maturity stage and total average tubule diameter (mm) according to maturity stage, in minke whale (*Balaenoptera acutorostrata*) males testes

Sample location	Maturity	Average	Min	Max	SD	N
PC	Immature	0.069	0.053	0.083	0.009	20
	Pubertal	0.116	0.069	0.209	0.043	20
	Mature	0.079	0.071	0.095	0.007	10
Total PC		0.090	0.053	0.209	0.035	50
P	Immature	0.066	0.051	0.083	0.008	30
	Pubertal	0.101	0.048	0.196	0.033	120
	Mature	0.138	0.036	0.292	0.037	630
Total P		0.130	0.036	0.292	0.040	780
C	Immature	0.123	0.095	0.143	0.016	10
	Pubertal	0.094	0.069	0.167	0.028	20
	Mature	0.147	0.060	0.405	0.037	729
Total C		0.145	0.060	0.405	0.038	759
Average P-C	Immature	0.076	0.051	0.143	0.023	60
	Pubertal	0.102	0.048	0.209	0.034	160
	Mature	0.142	0.036	0.405	0.038	1369

Table 10. Density (cover) of seminiferous tubules in testes of male minke whales (*Balaenoptera acutorostrata*), collected in the period 2003-2009, in Icelandic waters

	Immature	Pubertal	Mature	Total
Peripheral	32.00 (-) 1	49.00 (16.512) 6	65.44 (11.604) 73	64.16 (12.800) 77
Central	73.00 (-) 1	55.00 (12.192) 6	64.92 (11.480) 73	64.51 (11.612) 77
Combined	58.17 (19.623) 3	56.83 (16.133) 6	65.246 (9.472) 73	64.37 (10.566) 82
Difference C-P	41.00 (-) 1	6.00 (6.481) 6	0.53 (13.049) 73	0.35 (13.597) 82

FIGURES

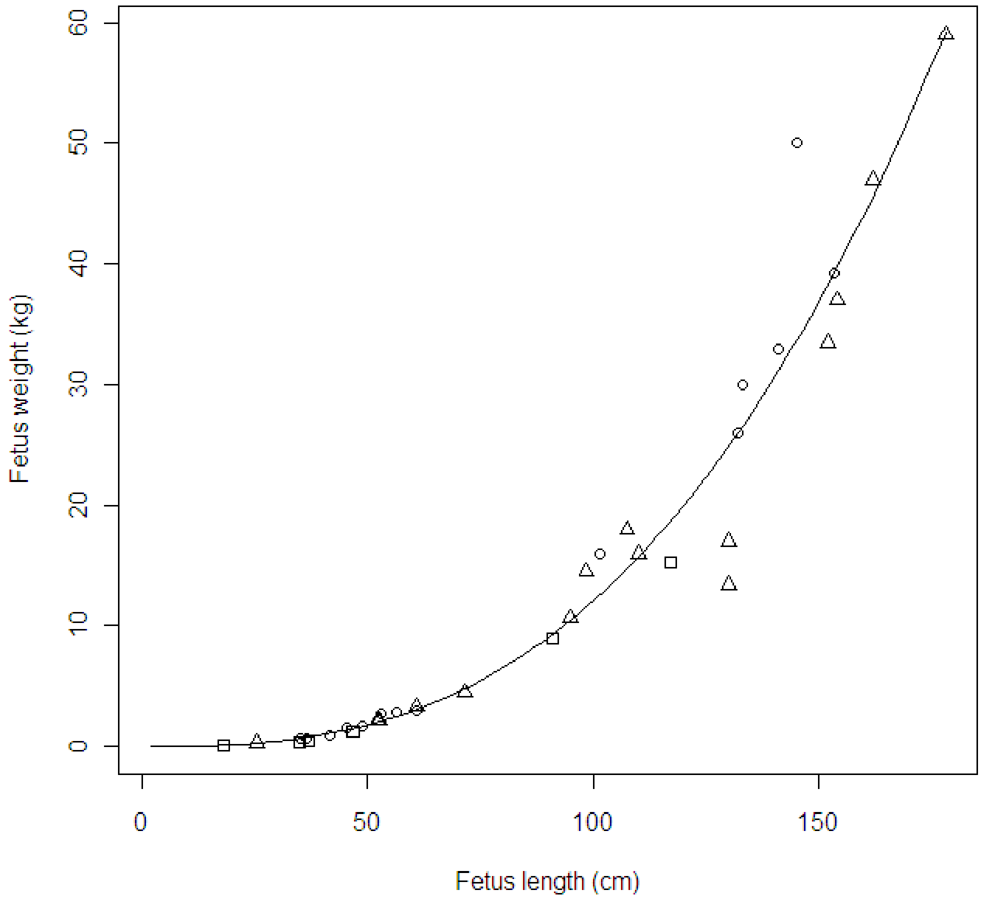

Figure 1. Foetus weight on length for minke whales (*Balaenoptera acutorostrata*) in Icelandic waters, in the period 2003-2009, triangles males, dots females and squares sex unknown.

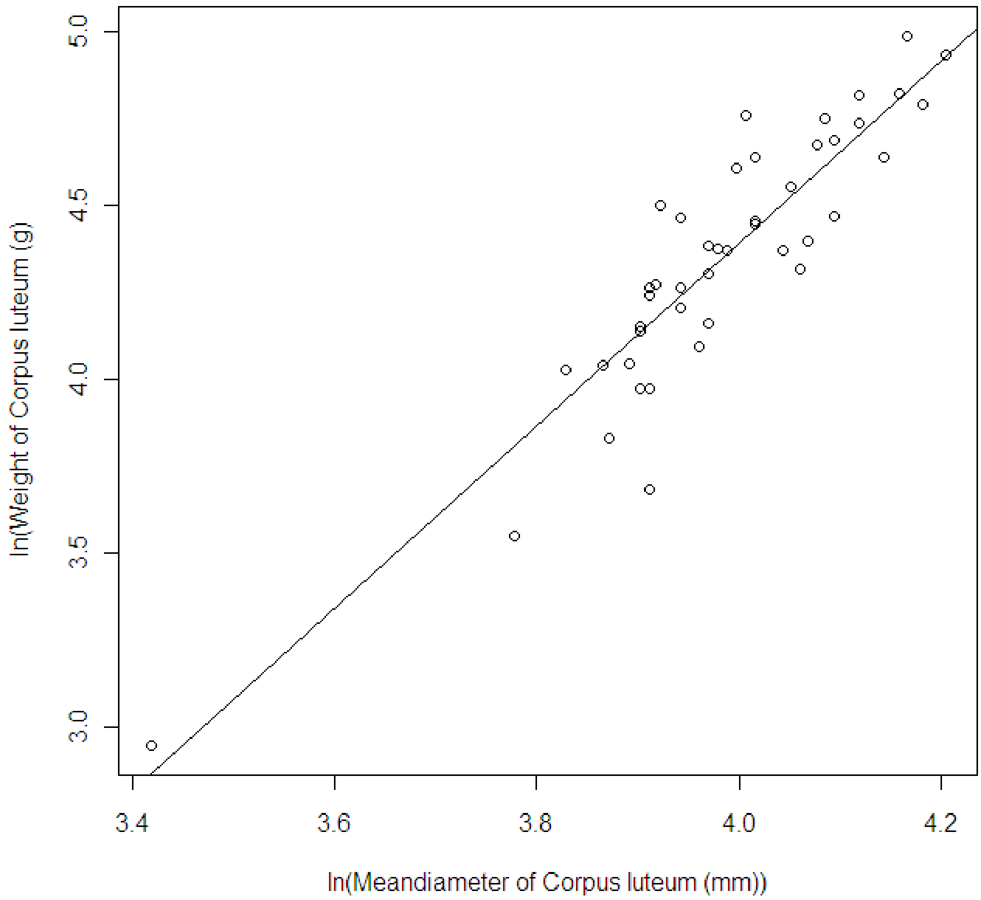

Figure 2. A power (*ln-ln*) relationship, between weight and mean diameter of *Corpus luteum* in ovaries of female minke whales (*Balaenoptera acutorostrata*) in Icelandic waters in the period 2003-2009.

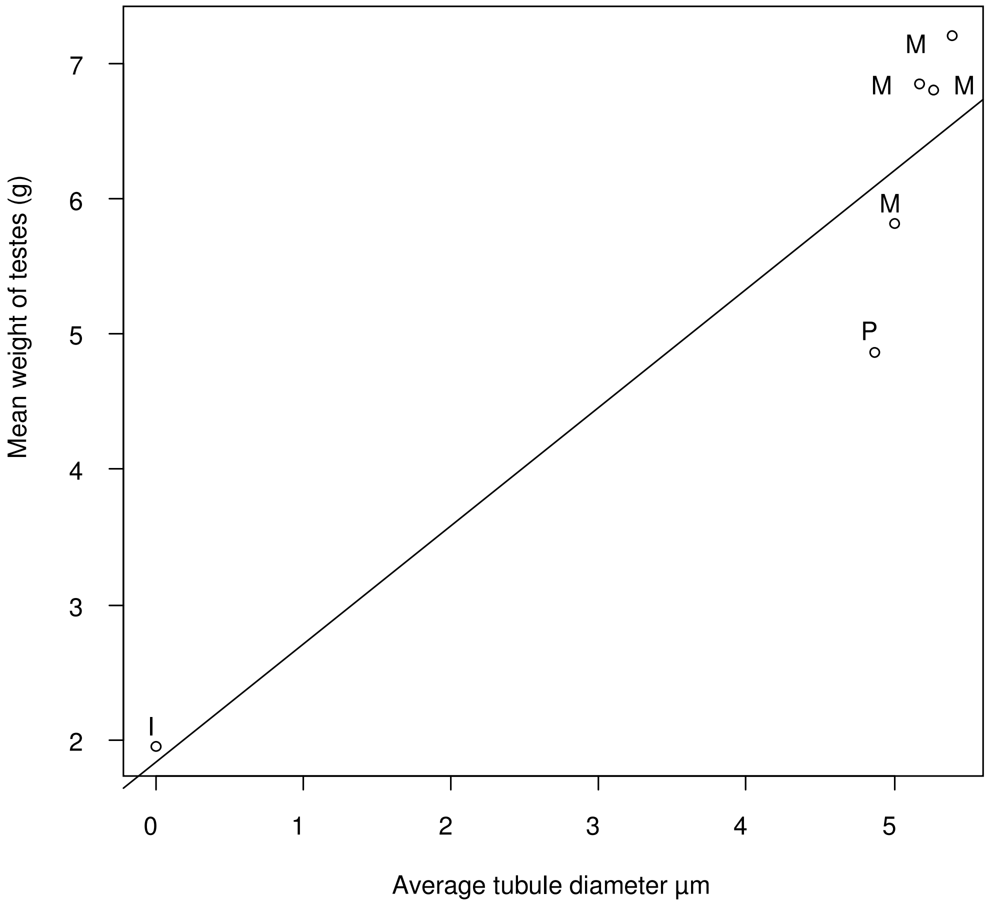

Figure 3. A *ln-ln* (power) relationship, between average seminiferous tubule and mean weight of testes in minke whale (*Balaenoptera acutorostrata*) males, caught in Icelandic waters in 2003-2009, both axes are in a natural logarithmic scale, I, immature, P, pubertal and M, mature males.

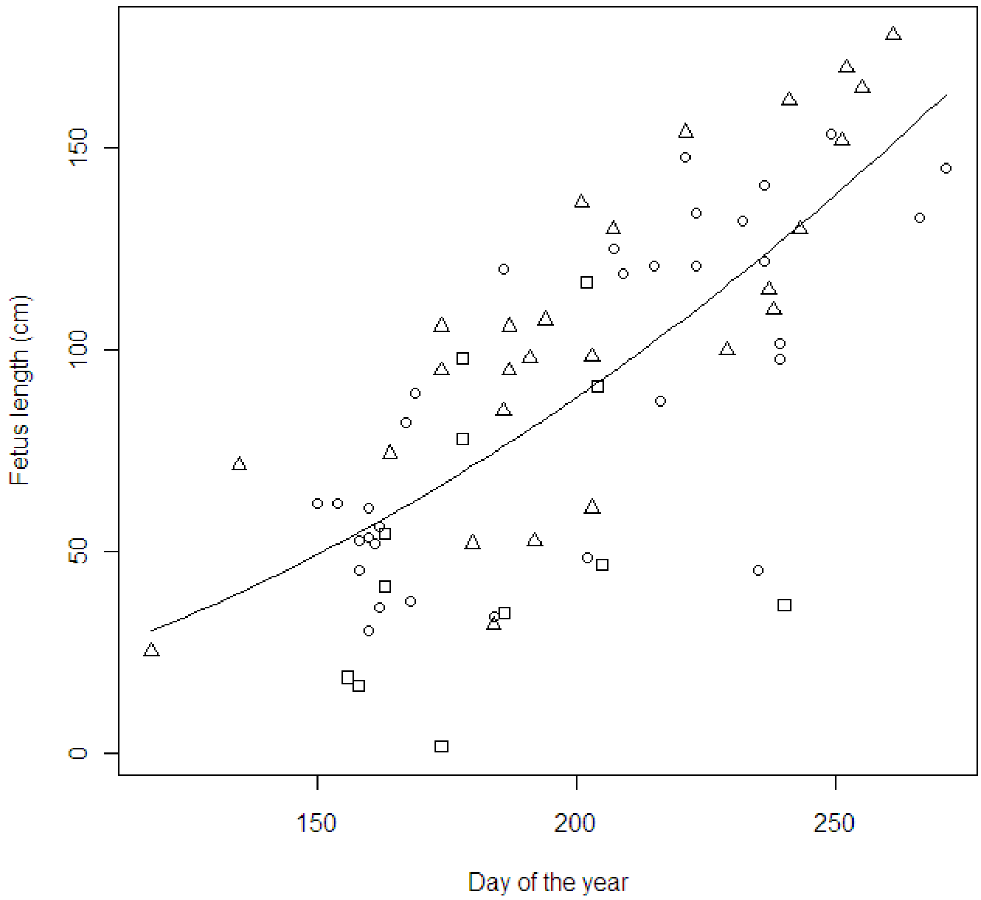

Figure 4. Curve-linear relationship between Julian day (1-365,) and minke whales (*Balaenoptera acutorostrata*) foetus length, squares sex unknown, triangles males and open dots females, from female minke whales caught in Icelandic waters in 2003-2009.

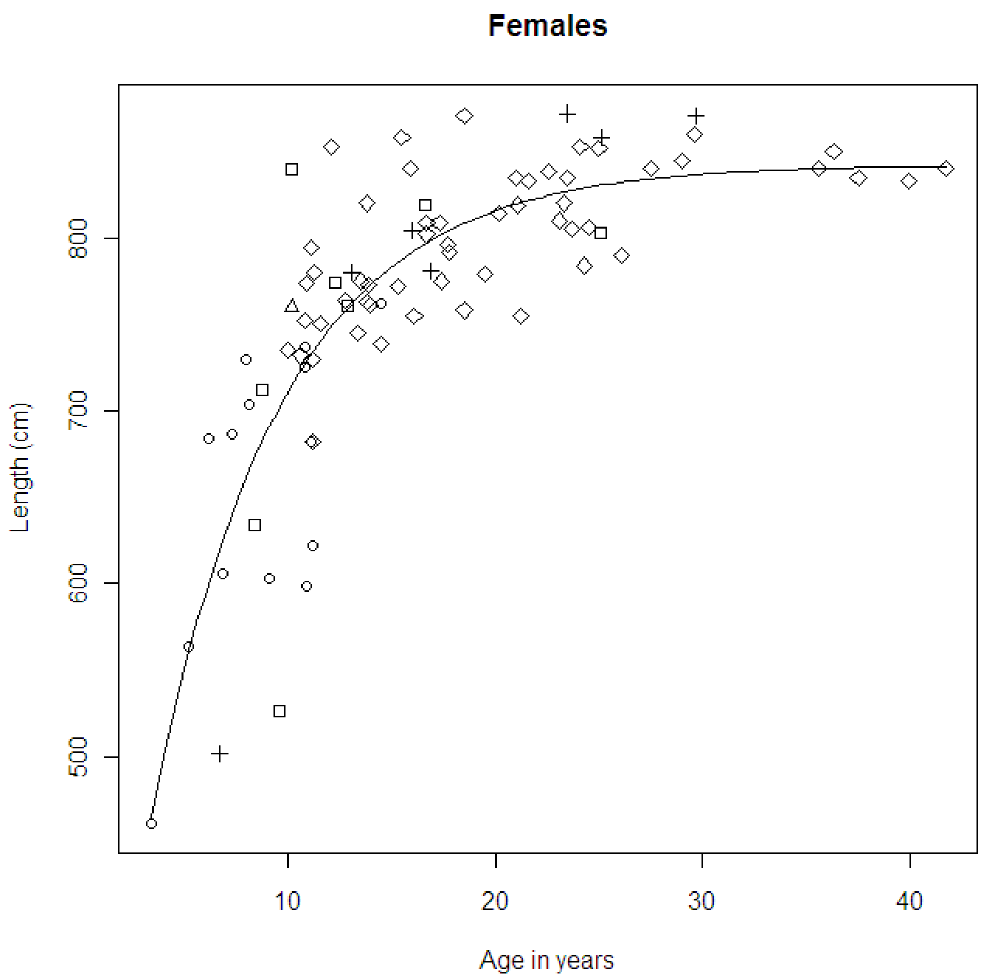

Figure 5. Mean body length with ASP-age in female minke whales (*Balaenoptera acutorostrata*) from Icelandic waters, caught in the period 2003-2009, (squares) no-information, (circles) immatures, (triangles) pubertal, (plus) mature and (diamond) pregnant.

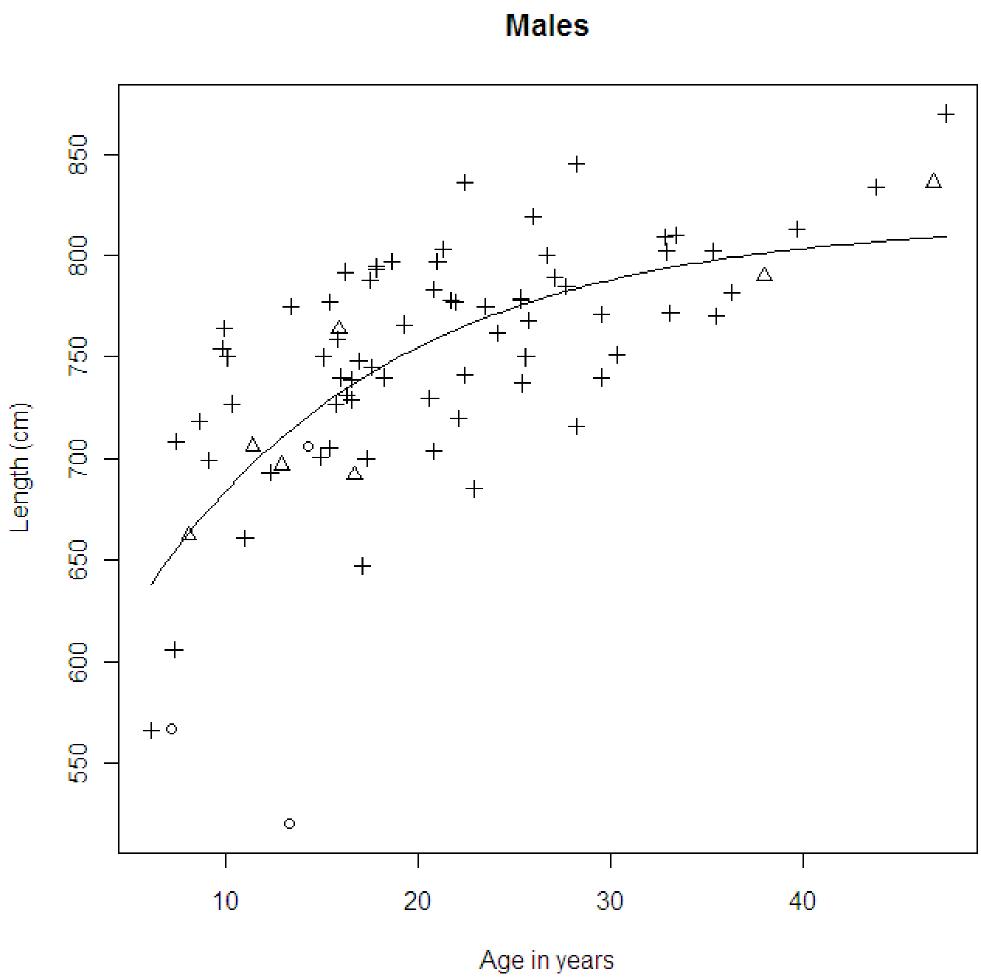

Figure 6. Mean body length with ASP-age in male minke whales (*Balaenoptera acutorostrata*) from Icelandic waters, caught in the period 2003-2009, (circles) immatures, (triangles) pubertal and (plus) mature.

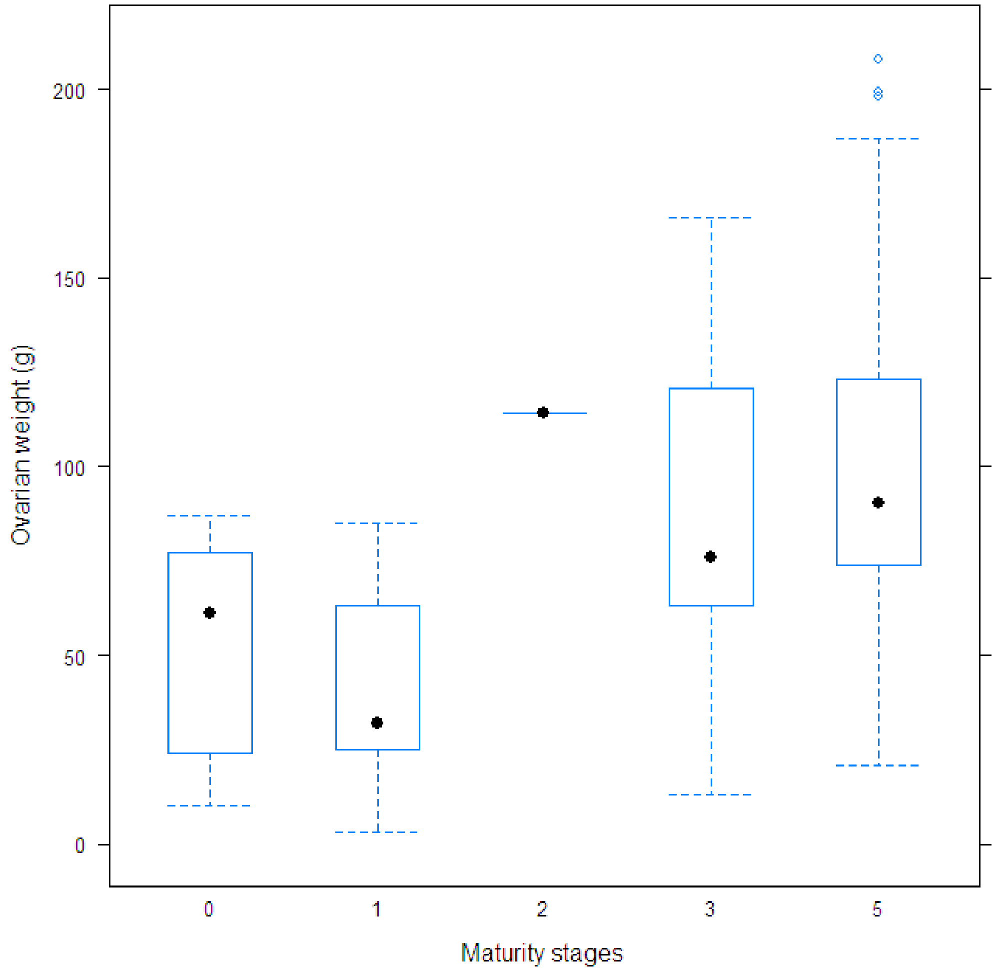

Figure 7. Mean ovarian weight in relation to maturity stages of female minke whales (*Balaenoptera acutorostrata*), 0, no information, 1, immature, 2, pubertal, 3, mature and 5, pregnant.

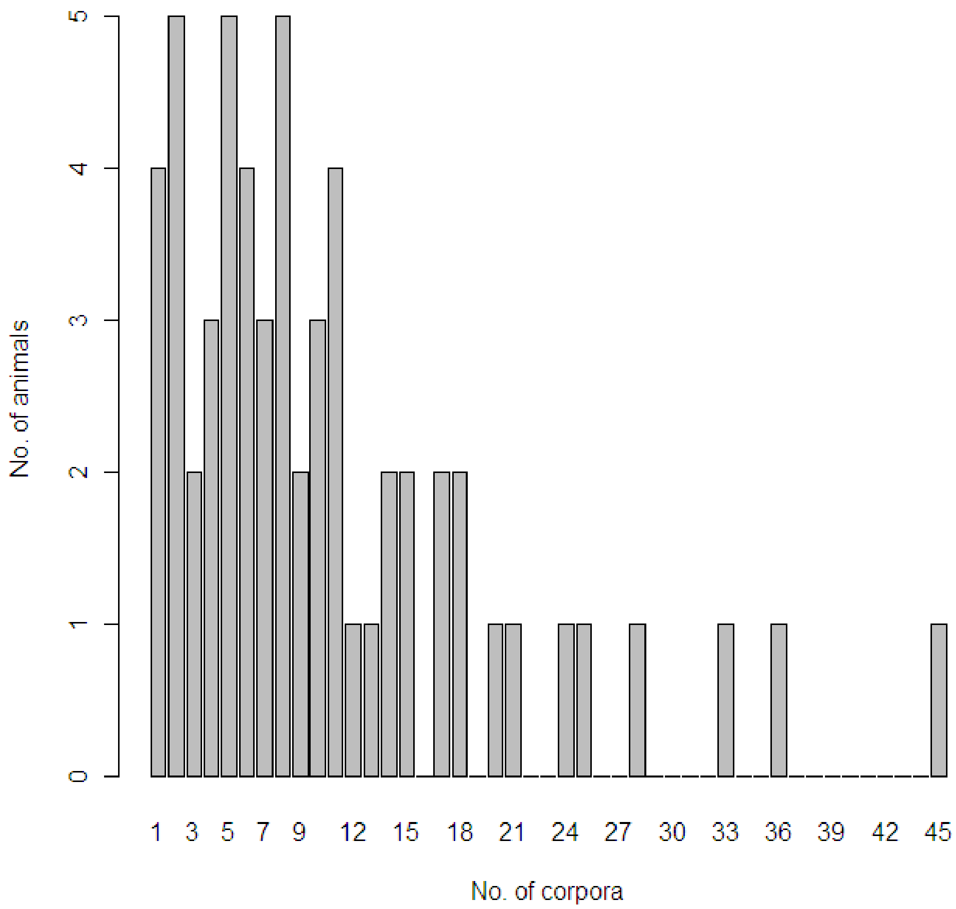

Figure 8. Frequency distribution, of number of corpora (*Corpus luteum, Corpora albicantia and Corpora atretica*) in ovaries of female minke whales (*Balaenoptera acutorostrata*), caught in Icelandic waters in 2003-2009.

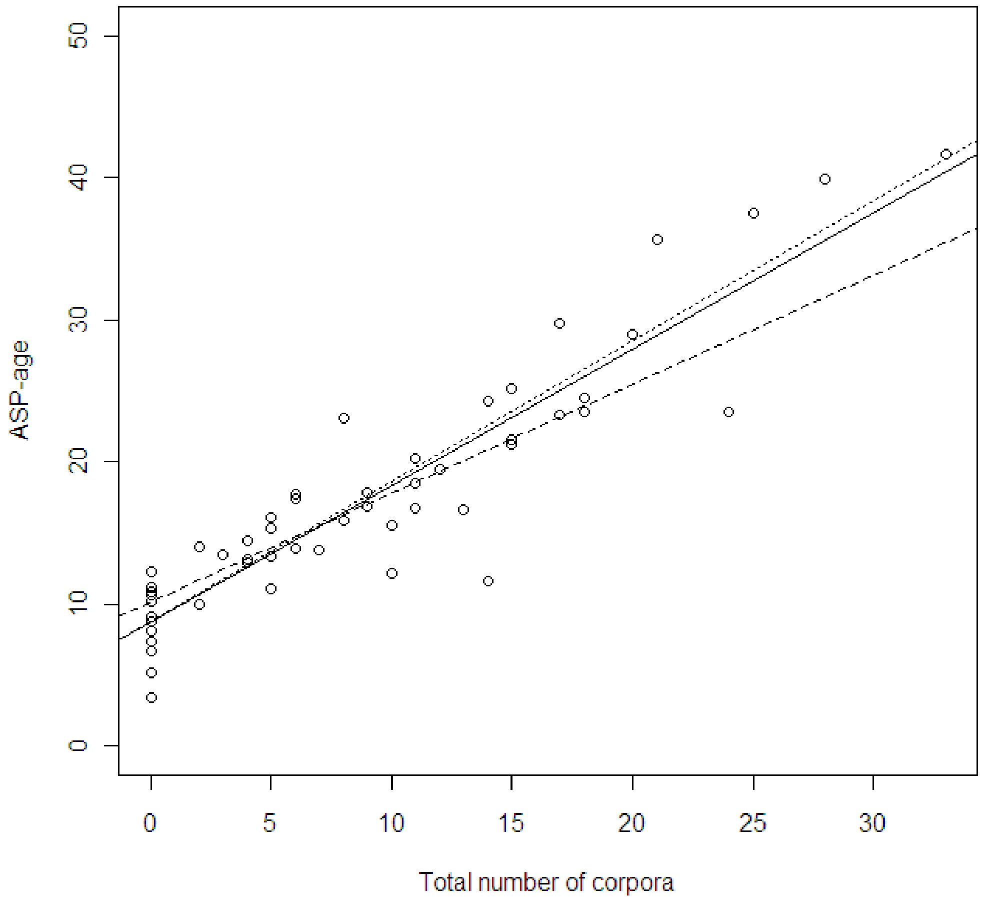

Figure 9. On the ordinate is ASP-age of minke whales (*Balaenoptera acutorostrata*) from Icelandic waters, caught in the period 2003-2009, determined with the method of racemisation of aspartic acid (ASP) from the whale eye lens, on the abscissa total number of corpora (*Corpora albicantina, Corpora atretica and Corpora lutea*), taken as a gospel. Unbroken line, ordinary regressions through data points, broken line, least trimmed square and dotted line, the resistant regression.

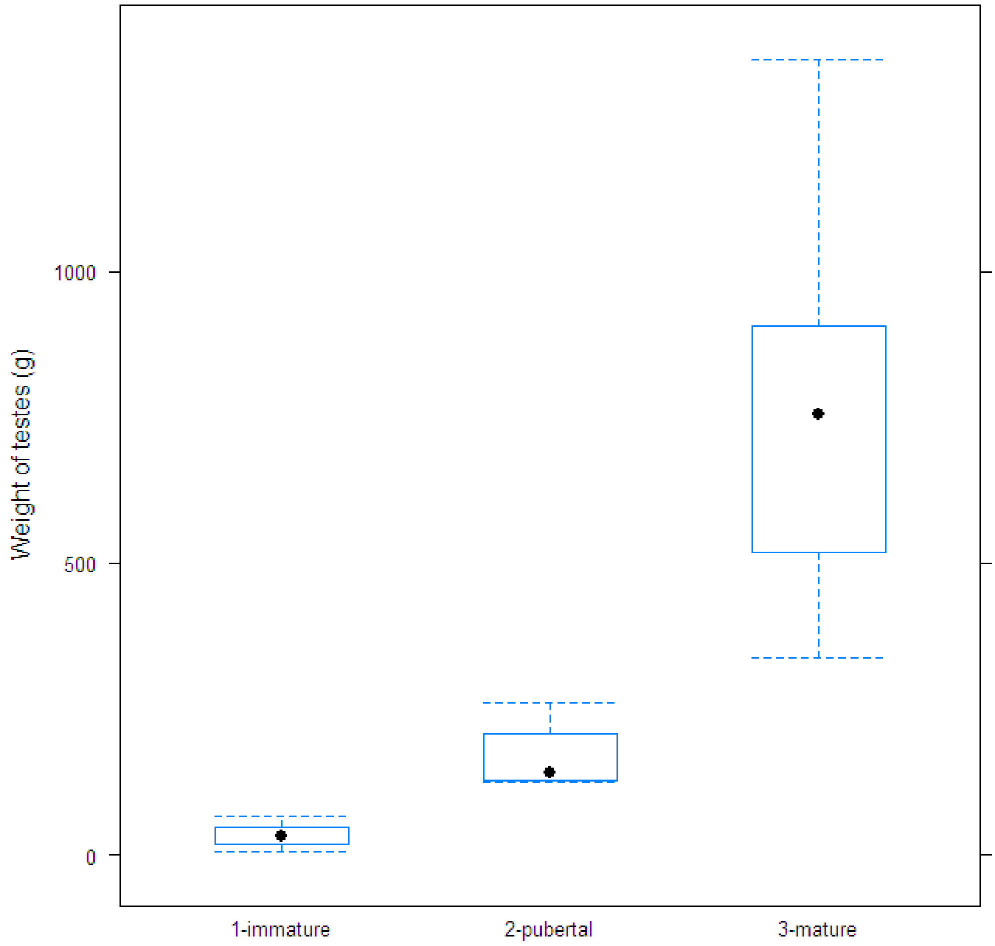

Figure 10. Mean weight of left and right testes in immature, pubertal and mature minke whale (*Balaenoptera acutorostrata*) males, caught in Icelandic waters in 2003-2009.

Comment [g1]: Single or combined?

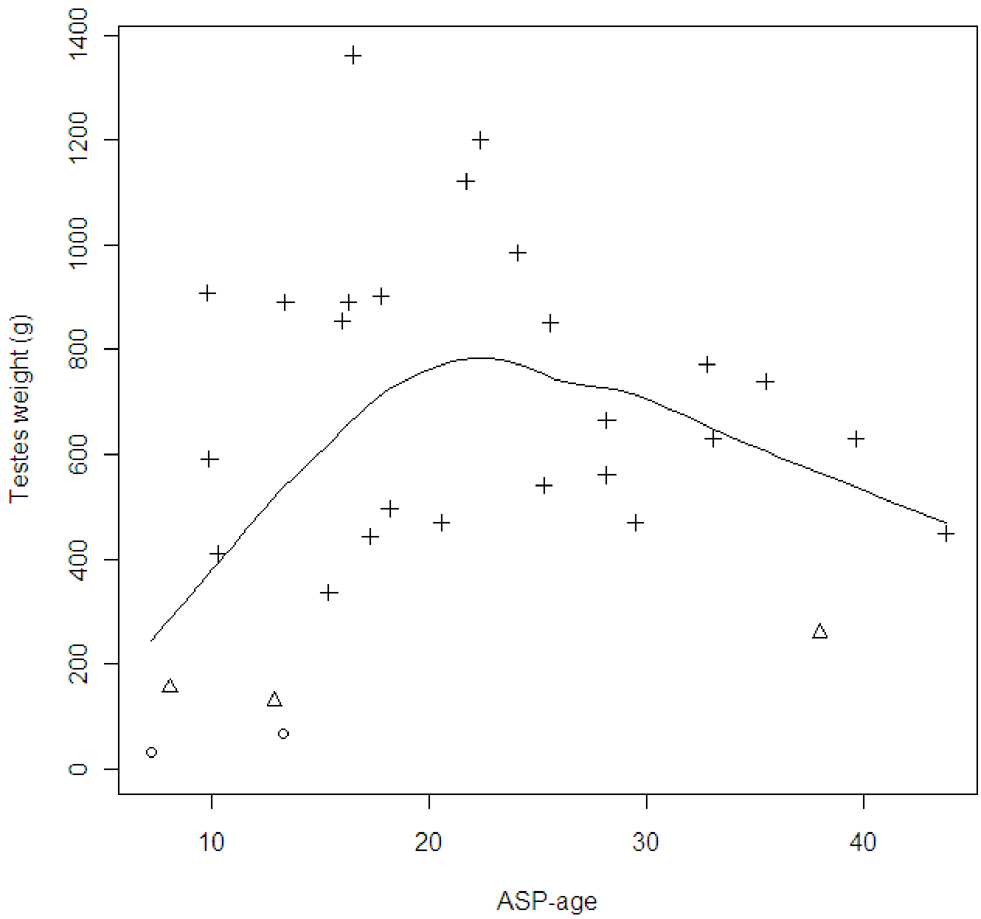

Figure 11. Mean weight of testes in relation to ASP-age, from; dots immature, triangles pubertal and plus sign, mature minke whale (*Balaenoptera acutorostrata*) males, caught in Icelandic waters in 2003-2009.

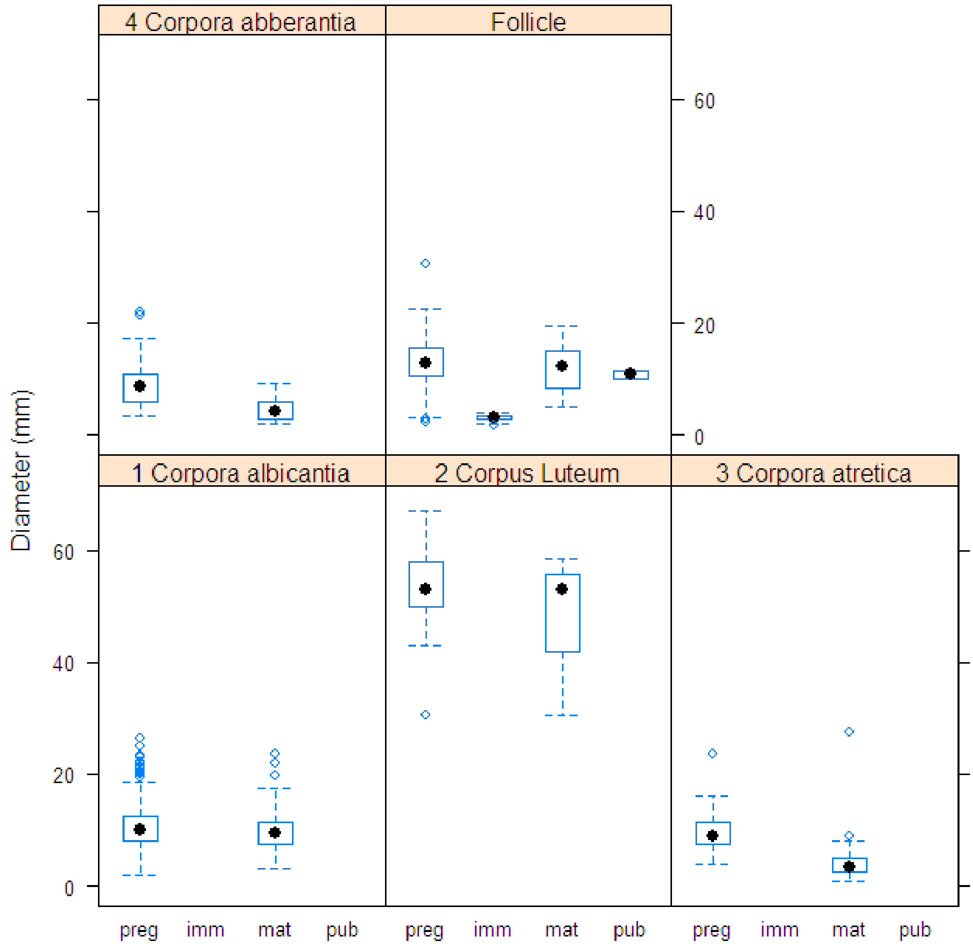

Figure 12. Diameter of the most abundant ovarian bodies, in the ovaries of female minke whales (*Balaenoptera acutorostrata*), caught in Icelandic waters in 2003-2009, in relation to the maturity stages, pregnant (preg), immature (imm), mature (mat) and pubertal (pub).

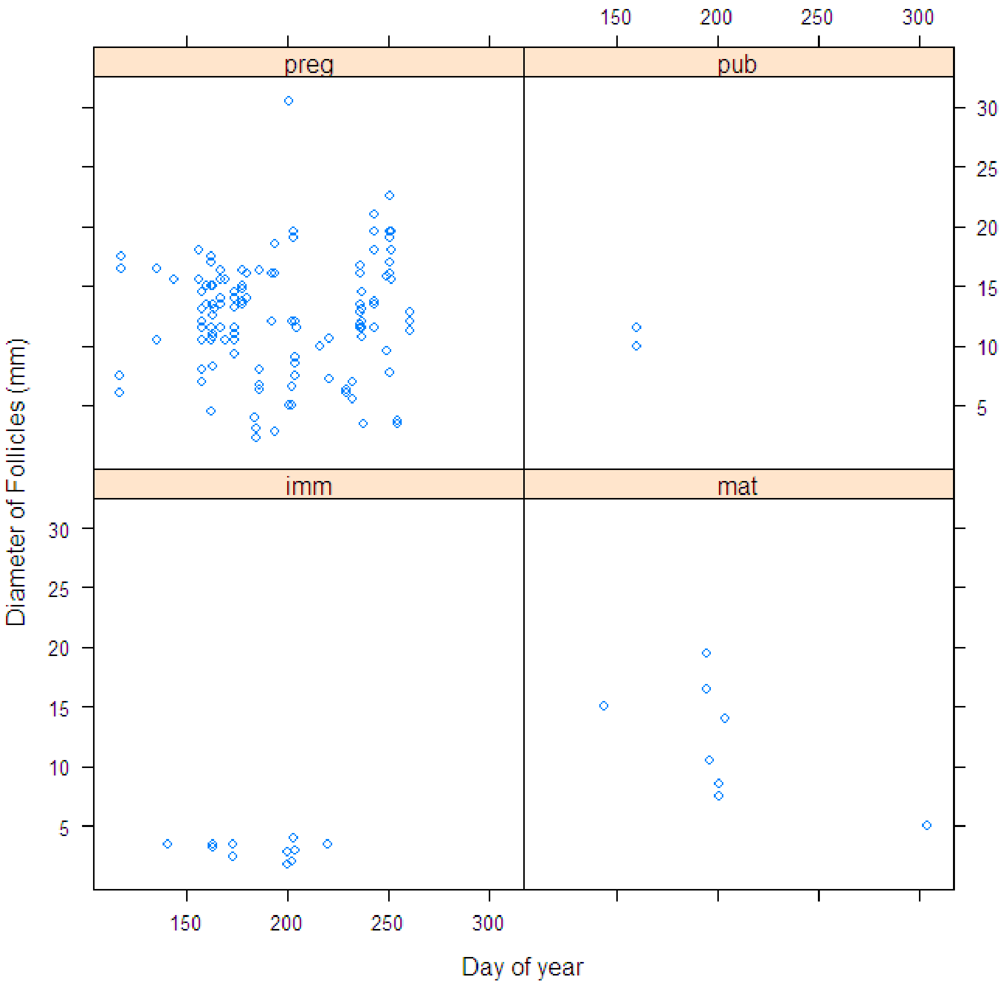

Figure 13. Follicle diameter, in relation to day of the year, in pregnant (preg), pubertal (pub), mature (mat) and immature (imm) female minke whales (*Balaenoptera acutorostrata*) cayght in Icelandic waters, in the period 2003-2009.

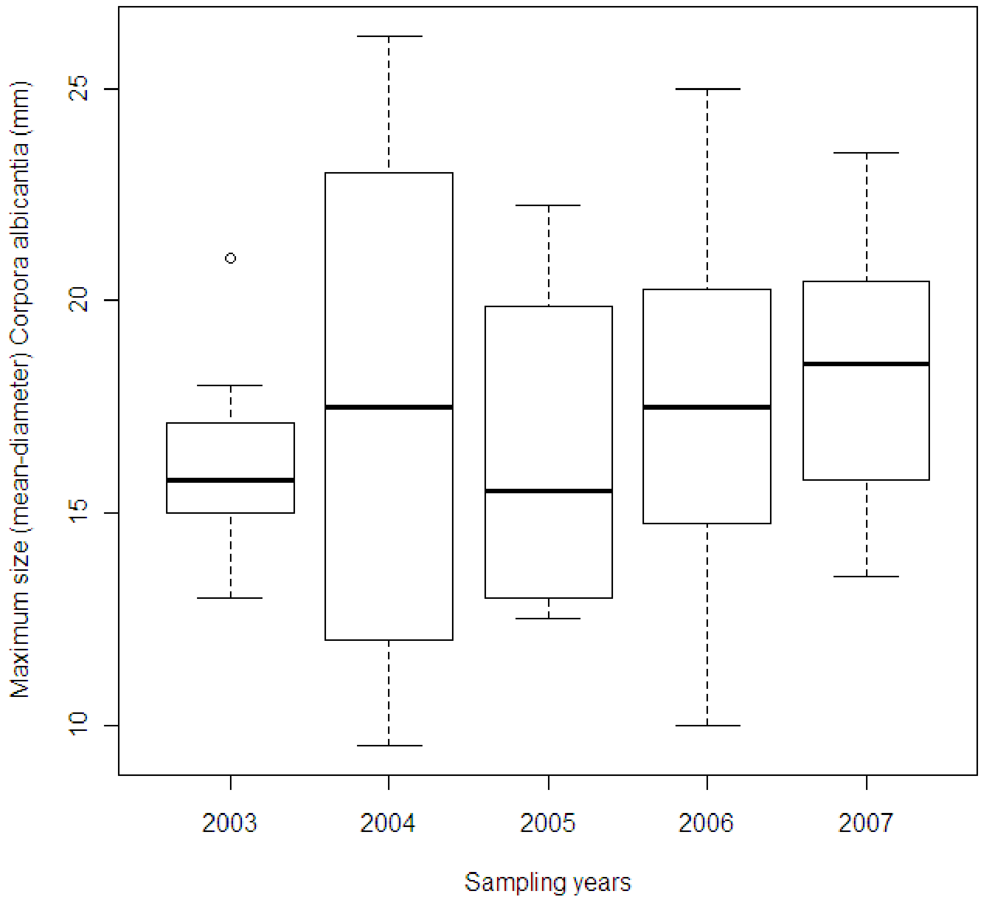

Figure 14. Mean, 50% interval of values and range of the maximum size *Corpora albicantia*, in each female minke whale (*Balaenoptera acutorostrata*), caught in Icelandic waters in the period 2003-2009.

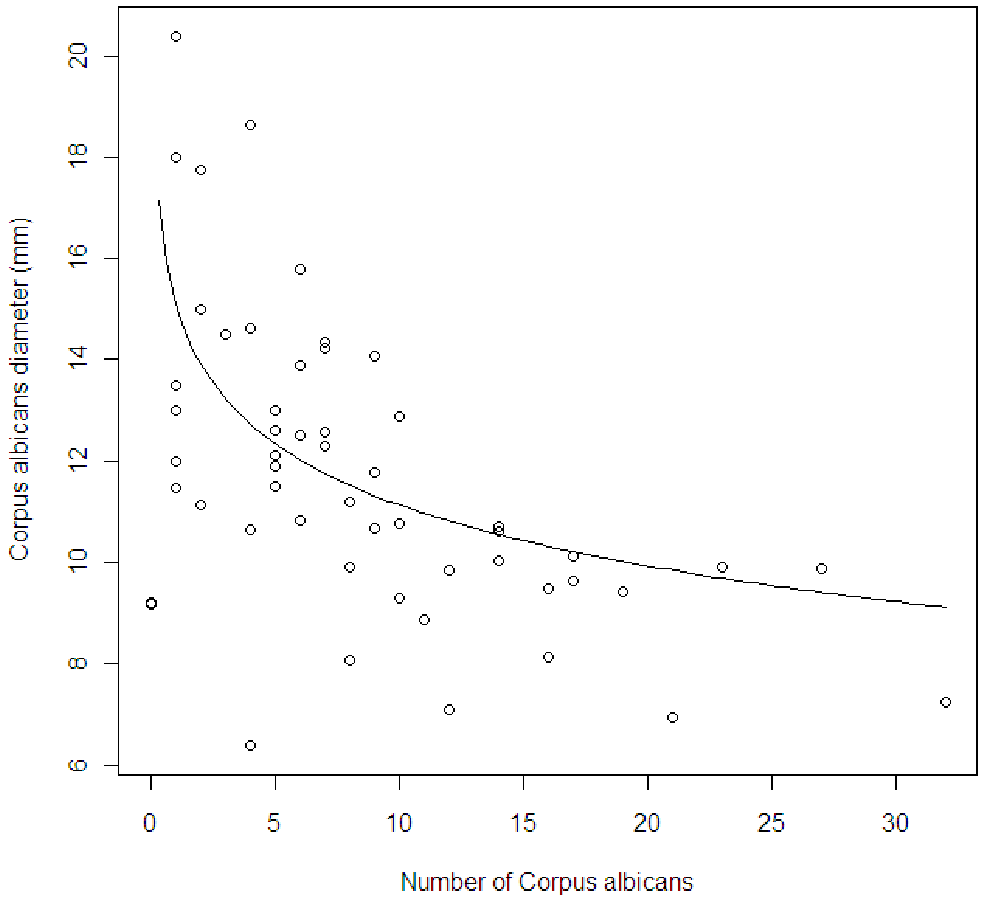

Figure 15. Relationship between mean *Corpus albican's* diameter and total number of Corpora albicantia in mature females minke whales (*Balaenoptera acutorostrata*) caught in Icelandic waters, in the period 2003-2009.

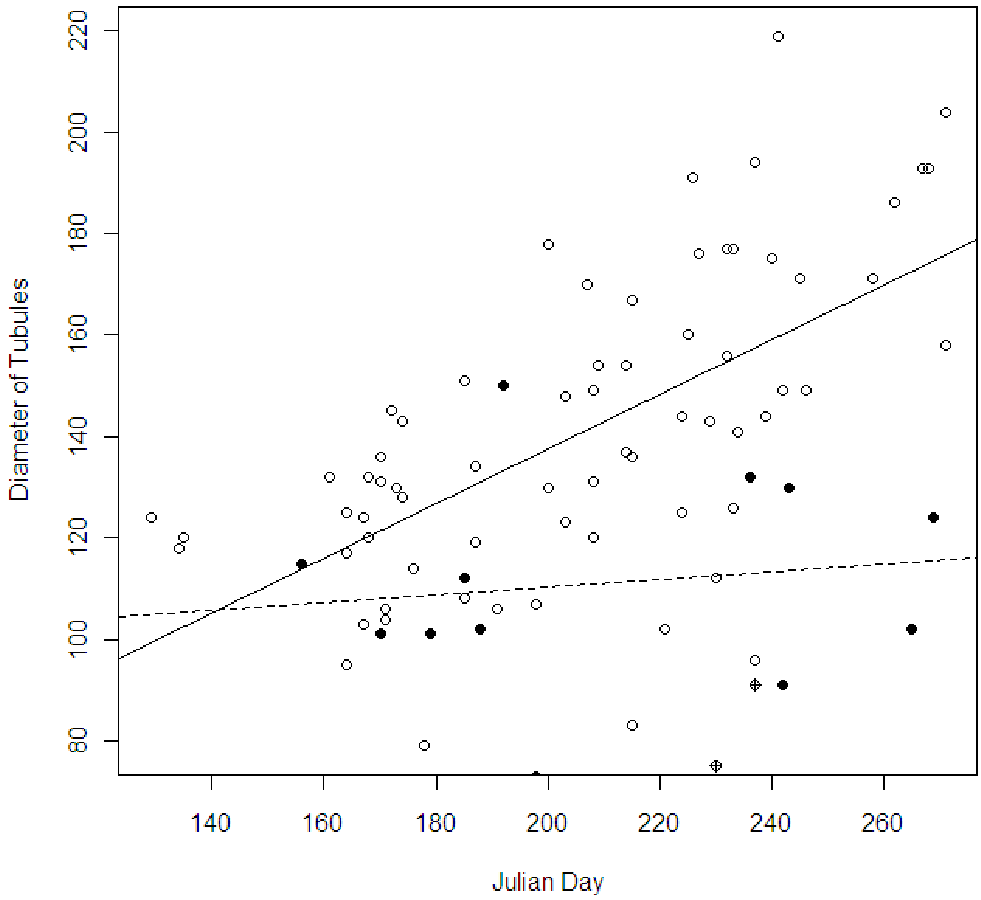

Figure 16. Distribution of measurements of the mean diameter (µm) of seminiferous tubules in testes of male minke whales (*Balaenoptera acutorostrata*) caught in Icelandic waters in 2003-2009, in relation to the day of sampling, mature animals open circles, pubertal animals black dots and immature animals open circle with a cross. Ordinary regression lines were fitted to the data for the mature (unbroken line) and pubertal (broken line) minke whales.

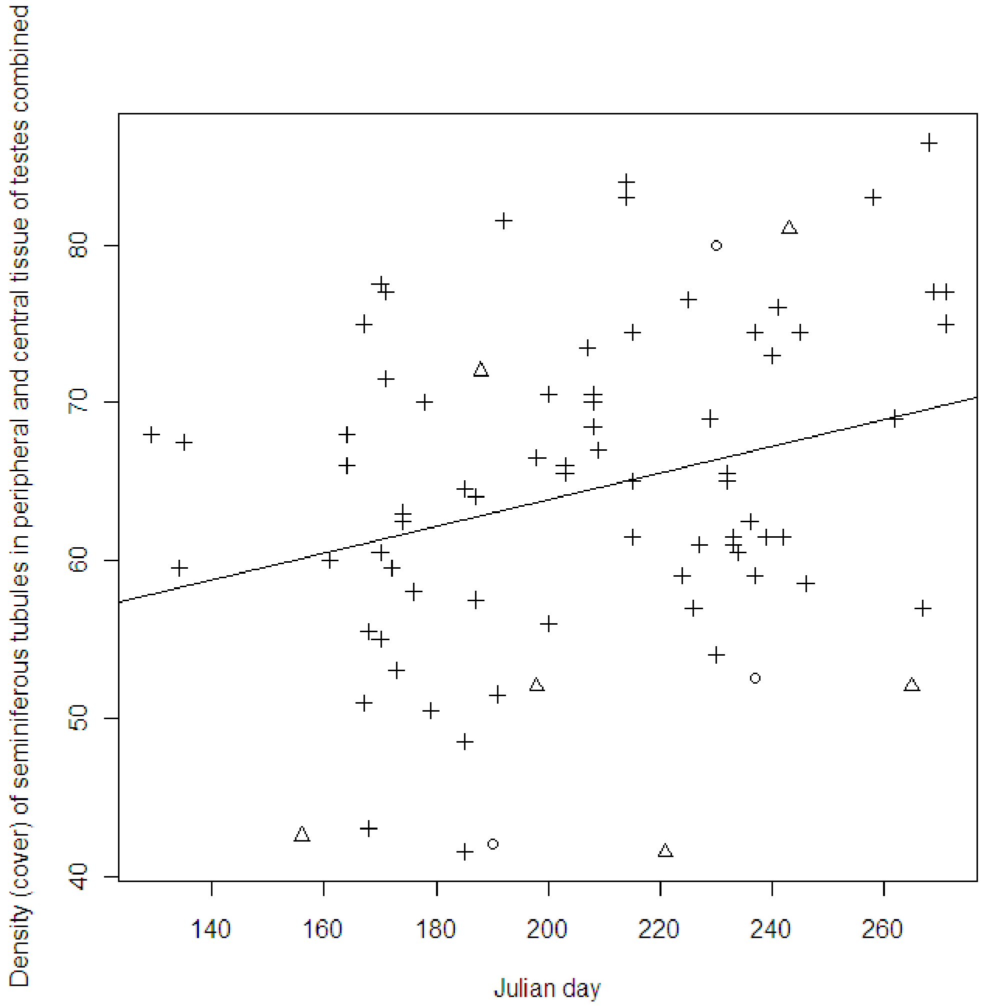

Figure 17. Changes in density (cover) of seminiferous tubules in testes of male minke whales (*Balaenoptera acutorostrata*) caught in Icelandic waters in the period 2003 - 2009, in relation to day of the year, (o) Immature, (Δ) pubertal a triangle and (+) mature.

REFERENCES

Bada, J.L., Brown, S. and Masters, P.M., 1980. Age determination of marine mammals based on aspartic acid racemization in the teeth and lens nucleus. *Rep. Int. Whal. Commn* (special issue), 3: 113-118.

Borchers, D.L., Pike, D.G., Gunnlaugsson, Th. And Víkingsson, G.A. 2009. Minke whale abundance estimation from the NASS 1987 and 2001 aerial cue-counting surveys taking appropriate account of distance estimation errors. *NAMMCO Sci. Publ.* 7:95-110.

Christensen, I., 1974. Undersokelser av vagehval i Barentshavet og ved Ost- og Vest Gronland i 1973. *Fiskets Gang* 60(14): 278-286.

Christensen, I., 1975. Preliminary report on the Norwegian fishery for small whales: expansion of Norwegian whaling to Arctic and northwest Atlantic waters, and Norwegian investigations of the biology of small whales. *J. Fish. Res. Board Can.*, 32(7): 1083-1094.

Christensen, I., 1981. Age Determination of Minke Whales, (*Balaenoptera acutorostrata*), from Laminated Structures in the Tympanic Bullae. *Report of the International Whaling Commission* 3: 245-253.

Collet, A. and Saint Girons, H., 1984. Preliminary study of the male reproductive cycle in common dolphins, *Delphinus delphis*, in the eastern North Atlantic. *Rep. Int. Whal. Commn* (special issue), 6: 355-360.

Perrin W.F and Donovan, W.F. (eds) 1984. Report of the Workshop. Rep. Int. Whal. Commn (Special Issue 6):1-24.

Everitt, B. S. and Hothorn, T. 2010. *A Handbook of Statistical Analyses Using R*. CRC Press. New York, 355 pps.

Gambell, R. 1968. Seasonal cycles and reproduction in sei whales of the Southern Hemisphere. *Discovery Rep*. 35: 31-134.

Halldorsson, S.D. and Víkingsson, G.A. 2001. Analysis of seasonal changes in reproductive organs from Icelandic harbour porpoises (*Phocoena phocoena*). *NAMMCO Sci. Publ.* 5: 121-142.

Harrison, R.J., 1969. Reproduction and reproductive organs. Ch. 8, pp. 253-348 in Andersen, H.T. (ed.). *The biology of marine mammals*. Academic Press, New York.

Horwood, J. 1990. *Biology and exploitation of the minke whale*. CRC Press, Inc. Florida, 238 pps.

Jonsgaard, A., 1951. Studies on the little piked whale or minke whale (*Balaenoptera acutorostrata*) Lacepede. Norsk Hvalfangsttidende, 40(5): 209-232.

Jonsgaard, Aa, 1962. Population Studies on the minke whale (B. acuto-rostrata) Lacepede. In E. D. le Cren and M. W. Holtgate, eds. *The explotation of natural animal populations.* Blackwell Publ., Oxford.

Kasuya, T. and Marsh, H., 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. Int. Whal. Commn* (special issue), 6:259-310.

Kinze, C.C., 1990. Marsvinet i danske forvande - utbredelse, yngleforekomst og trusler. Fauna och flora 85: 114-121.

Konradsson, A. and Sigurjonsson, J., 1989. Studies on Growth Layers in Tympanic Bullae of Fin Whales (*Balaenoptera physalus*) caught off Iceland. *Report of the International Whaling Commission*, 39: 277-279.

Larsen, F. and Kapel, F.O., 1982. Norwegian minke whaling off West Greenland, 1976-80 and biological studies of West Greenland minke whales. *Report of the International Whaling Commission*, 32: 263-274.

Larsen, F., 1984. Reproductive parameters of the minke whale, *Balaenoptera acutorostrata*, off West Greenland. *Rep. Int. Whal. Commn* (special issue), 6: 233-236.

Laws, R.M. 1961. Reproduction, growth and age of Southern fin whales. Discovery Rep. 31:327-486.

Lockyer, C., 1972. The age at sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. *J. Cons. int. Explor. Mer* 34(2): 276-294.

Lockyer, C., 1976. Investigation of the ear plug of the southern sei whale (*Balaenoptera borealis*) as a valid means of determining age. *J. Cons. int. Explor. Mer*. 36: 259-270.

Lockyer, C., Gambell, R. and Brown, S.G., 1977. Notes on Age Data of Fin Whales Taken off Iceland, 1967-74. *Report of the International Whaling Commission*, 27: 427-440.

Lockyer, C. and Sigurjónsson, J. 1992. Author's summary f SC/F91/F8: The Icelandic Fin Whale, (*Balaenoptera physalus*): Biological Parameters and Their Trends Over Time. Rep. Int. Whal. Commn. 42: 617-618.

Mackintosh N.A. and Wheeler, J.F.G 1929. Southern blue and fin whales. *Discovery Rep*. 1: 257-540.

Marine Research Institute 2003. A programme for a two year feasibility study on cetaceans in Icelandic waters. IWC SC/55/O2-revised. Reykjavik, 63 pps.

Mitchell, E. and Kozicki, V.M., 1975. Supplementary information on minke whale (*Balaenoptera acutorostrata*) from Newfoundland fishery. *J. Fish. Res. Board Can*. 32(7): 985-994.

Mitchell, E. and Kozicki, V.M., 1984. Reproductive condition of male sperm whales, *Physeter macrocephalus*, taken off Nova Scotia. *Rep. Int. Whal. Commn* (special issue), 6: 243-252.

Ohsumi, S. 1986. Earplug transition phase as an indicator of sexual maturity in female Antarctic minke whales. Sci. Rep. Whales Res. Inst. 37: 17-30.

Omura, H. and Sakiura, H. 1956. Studies on the little piked whale from the coast of Japan. *Sci. Rep. Whales Res. Inst*. 11(1):1-37.

Pike, D.G., Gunnlaugsson, TH., Víkingsson, G.A., Desportes, G. and Bloch, D. 2009a. Estimates of the abundance of minke whales (Balaenoptera acutorostrata) from Faroese and Icelandic NASS shipboard surveys. *NAMMCO Sci. Publ*. 7: 81-93.

Pike, D.G., Paxton, C.G.M., Gunnlaugsson, Th. and Víkingsson, G.A. 2009b. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986-2001. *NAMMCO Sci. Publ*. 7: 117-142.

Purves, P.E., 1960. The use of the ear plug in age determination in whales. XVth International Congress of Zoology, Sect. III, Paper.

Reeves, R.R., Stewart, B.S., Clapham, P.J. and Powell, J.A. 2002. *Guide to marine mammals of the World.* Alfred A. Knopf, New York, 528 pps.

Sæmundsson B. 1931. Fiskirannsóknir 1929-1930: skyrsla til stjórnarráðsins. Andvari – *Tímarit Hins íslenska þjóðvinafélags* 56: 48-110.

Sæmundsson B. 1937. Fiskirannsóknir 1936-1937: skyrsla til stjórnarráðsins. Andvari – *Tímarit Hins íslenska þjóðvinafélags* 62: 22-61.

Sigurjónsson, J. and Víkingsson, G.A., 1998. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. *J. Northw. Atl. Fish. Sci.,* 22: 271-287.

Sigurjónsson, J., 1980. A preliminary note on ear plugs from Icelandic minke whales. *Report of the International Whaling Commission*, 30: 193-194.

Sigurjónsson, J., 1982. Icelandic minke whaling 1914-1980. *Report of the International Whaling Commission*, 32: 287-295.

Sigurjónsson, J., 1988. Studies on age and reproduction in minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. *Rep. Int. Whal.comn*, 39, pp.461-462.

Sigurjónsson, Jóhann, Halldórsson, S.D. and Konráðsson, A., 1990. New information on age and reproduction in minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. *Rep. Int. Whal. Comn*, (SC/42/NHMi27). 18 pps..

Stenseth, N.C., Hoel, A.H. and Ingunn, B. (red) 1993. Vågehvalen. Ad Notam, Gyldendal. Oslo, 358 pps.

Sukhovskaya, L.I., Klevezal, G.A., Borisov, V.I. and Lagerov, S.I. 1985. Use of bone layers for age determination of minke whales, *Balaenoptera acutorostrata*, *IWC Doc. SC/36/Mi 6, International Whaling Commission*, Cambridge, England (mimeograph)

Verzani, J. 2005. *Using R for Introductory Statistics.* Chapman & Hall/CRC. Boca Raton, 414 pps.

Víkingsson, G.A. 2004. Hrefna. In Hersteinsson, P. (ed.). *Íslensk spendýr*. Vaka-Helgafell. Reykjavík, 344 pps.(in Icelandic).

Víkingsson, G.A., Ólafsdóttir, D., Gunnlaugson, Þ., Pampoulie, C., Halldórsson, S.D., Galan, A., Svanson, V., Kjeld, M., Auðunsson, G.A. and Daníelsdóttir, A.K. 2008. Research programme on common minke whales (Balaenoptera acutorostrata) in Icelandic waters. A progress report May 2008. IWC 2008 SC/60/O13, 18 pps.

Víkingsson, G.A. and Elvarsson, B.Þ. 2010. Recent changes in diet composition of minke whales (Balaenoptera acutorostrata) in Icelandic waters. NAMMCO SC/17/AS/06, 13 pps.

Yunker, G.B., Hammill, M.O., Gosselin, J.-F., Dion, D.M. and Schreer, J.F. 2005. Foetal growth in north-west Atlantic grey seals (*Halichoerus grypus*). *J. Zool., London* 265: 411-419.