

## **Growth and reproduction of common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters**

Erlingur Hauksson<sup>1</sup>, Gísli A. Víkingsson<sup>1</sup>, Sverrir Daniel Halldórsson<sup>1</sup>, Droplaug Ólafsdóttir<sup>1</sup>  
Nynne Hjort Nielsen<sup>2</sup> and Jóhann Sigurjónsson<sup>1</sup>.

*Programme for Whale Research, Marine Research Institute, P.O.Box 1390, Skúlagata 4, 121  
Reykjavik, Iceland*

*<sup>2</sup>Greenland Institute of Natural Resources, Postbox 570, 3900 Nuuk, Greenland*

### **ABSTRACT**

As a part of a special permit research program reviewed by the IWC Scientific Committee in 2003 a total of 200 minke whales (including 10 struck and lost) were caught for scientific purposes during 2003-2007... The scientific sampling of minke whales was distributed temporally and spatially in accordance with the relative distribution of common minke whales around Iceland, but the commercial harvest was more opportunistic. The overall (female/male) sex ratio was 1.30/1 and 1.20/1, for foetus and 0+ whales respectively, not significantly different from 1:1. A new method of aging minke whales in Icelandic waters, was used, the racemisation of aspartic acid from the whale's eye lens, giving the mean age for females and males as 18 and 21 years respectively, and the oldest female and male 42 and 47 years respectively. Standard length at birth was estimated with the von Bertalanffy growth model as about 2 meters and females grew faster and attained larger size than males. Asymptotic standard length was 795 and 842 cm for males and females respectively. Estimated age and standard length at sexual maturity was 7 and 10 years and 639 and 713 cm for males and females respectively. Pronounced seasonality was observed in testes weight and in the diameter and cover of seminiferous tubules, 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., About 91% of mature females were reproducing and 9% anoestrous, indication a predominantly annual reproductive cycle. The study confirmed earlier findings of parturition and conception occurring in mid-winter and gestation about 11 months. However, there was great temporal variability in parturition and conception, indicated by high variability of standard length of foetus in relation to day of the year...One minke whale female of total of 72 pregnant females had twin foetuses (1.4%).

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

---

<sup>1</sup> Present address: The Icelandic Meteorological Office, Bústaðavegur 9, 150 Reykjavík.

## INTRODUCTION

According to aerial and shipboard surveys conducted regularly since 1986 common minke whale is Iceland's most numerous baleen whale (Borchers et al. 2009; Pike et al. 2009a,b). Common minke whales have been exploited in Icelandic waters since 1914 (Sigurjónsson 1982). 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 well 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, which reached the Icelandic waters too, the average Norwegian catch off Iceland in the period 1961-1972 was around 110 whales, however, after the extension of the Icelandic fisheries jurisdiction the catches became insignificant. On the average the Norwegian and Icelandic catches numbered around 200 common minke whales in the years 1960-1985.

Information on biology of the common minke whale in Icelandic waters, including data on age and reproduction, were presented by Sigurjónsson (1982, 1988) and Sigurjónsson et al. (1990), based on material from the coastal common minke whale fishery in the years 1977-78, which was collected by whalers in cooperation with scientists of MRI, in the whaling seasons 1979 through 1985. The distribution of common minke whales is usually closer to coast than that of larger rorquals. Migrations in Icelandic waters are not well documented, however, minke whales have been observed in all parts of Icelandic coastal 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 May to September (Sigurjónsson and Víkingsson 1997), with high abundance spots in Faxaflói and off the Southeast-coast. Marked segregation by the sexes has been observed in the catch, (SC/F13/SP14). Common minke whales have been observed to feed on a broad spectrum of prey and are more piscivorous than the other larger rorquals (e.g. Horwood 1990, Haug et al 1995). In Icelandic waters, the most important prey species include sand-eels (*Ammodytes sp.*), herring (*Clupea haerengus*), capelin (*Mallotus villosus*), euphausiids and several species of larger bony fishes, in Icelandic waters (Sigurjónsson and Víkingsson 1998; Víkingsson and Elvarsson 2010, SC/F13/SP2). Christiansen et al (SC/F13/SP8) showed that minke whales being capital breeders aim to maximize energy storage and food intake, while on the feeding grounds in Icelandic waters. The total amount of energy deposited into blubber through the feeding season was estimated about 13 GJ, for an average common minke whale. 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, standard length at maturity of females and males are 7 – 7.5 and 6.5 – 7 meters respectively. Maximum standard 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, and at least four organs/tissues have been studied in relation to aging, the *Tympanic bulla*, the ear plug, mandibles 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, is both technically difficult and tedious. Age determination of minke whales by using ear-plugs has also been shown to be difficult. Minke whale ear plugs are very hard to get intact from animals and not giving as reliable

results as for example in the fin whale (*Balaenoptera physalus*) and sei whale (*Balaenoptera borealis*) (Lockyer 1976, Lockyer et al. 1977, Sigurjónsson 1980, (Olsen & Sunde 2002; Christensen 1992). The *Tympanic bulla* is somewhat less complicated, and the application in the field and the laboratory is less time consuming than the preparation and reading of the ear plugs. However, the use of this method has severe limitations and seems to be reliable only up to a certain age (Sigurjónsson 1980, Christensen 1981). Similar results have been obtained for other species. Thus, there was observed a bad fit between bulla growth layers number and corpora counts in fin whales (Konradsson and Sigurjónsson 1989). Sukhovskaya et al. (1985) found that bulla layers of Antarctic minke whales gave consistently lower counts than the ear plugs from the same animals. Larsen and Kapel (1982) also reported difficulties in discriminating between primary and secondary growth layers in the bulla, and found it affect the readability. The use of mandible growth layers is not feasible for for age determination of minke whales (Olsen et al. 2003). Exhaustive attempts to use both ear plugs and bullae for age determination in this project were unsuccessful (SC/F13/SP1). In light of these problems, it was decided to use a relatively new method for aging minke whales based on the racemisation of aspartic acid from the whale's eye lens. This method has been used on other cetacean species such as bowhead whales (George, et al. 1999) and fin whales (Nielsen et al. 2012) and also on minke whales off Norway (Olsen & Sunde 2002) The general methodology applied is given in Bada et al. (1980).

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. The seminiferous tubules also take more space inside the testes tissues, their cover or density increases (Collet and Saint Girons 1984; Kasuya and Marsh 1984; Kinze 1990; Neuenhagen et al. 2007). 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 scientists. Some 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 was generally easier, as each ovulation and pregnancy leaves a permanent scar in the ovary, the *Corpus albicans* and *Corpus abberance*. Based on the presence or absence of such scars, females are usually classified as either immature or mature, mature and "resting" (anoestrous with no *Corpus luteum*) and pregnant if *Corpus luteum* was detected in the ovaries and/or foetus was found in the uterus. The reproductive history can also be read from the numbers and characteristics of corpora found in the ovaries (C. Lockyer 1984). Ovaries in female cetaceans do often 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 Ocean and connected waters, but knowledge on their reproductive biology in Icelandic waters has been rather limited. In this paper we present our findings of biological parameters as growth and reproduction of common minke whales, 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 common 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 as a part of the Icelandic minke whale research programme in 2003-2007 (Marine Research Institute 2003) with minor additions from the commercial whaling in years 2006, 2008 and 2009. From whaling operations, either scientific or commercial, in the period 2003-2009, a total of 208 minke whales samples were collected, in the period 2003-2009, 107 females and 101 males (Table 1). The sampling design of the special permit research programme attempted to reflect seasonal and geographical distribution of the species in Icelandic waters, while the commercial catch was mainly originated from Faxaflói bay W-Iceland (SC/F13/SP1). The collection of material and field studies in the scientific programme was conducted, by the MRI whale scientists. The total sample covers the period April- November with highest sampling effort during June-August in accordance with seasonal occurrence of the species in Icelnadic waters. (Fig. 1). Five sampling vessels were operated in different coastal areas (SC/F13/SP1), with cruise leaders from the Marine Research Institute (MRI). The total sample of the study includes 208 minke whales thereof 190 from the research programme. 184 sex-organs, 69 foetus and 202 eyes were collected (Table 2). Eyes were stored as soon as possible at -20°C. Ovaries and testicles were labeled, fixed and stored in 10% neutral formalin solution.

### Age determination

Age was determined with the method of racemisation of aspartic acid (ASP) from the whale's eye lens; see (Marine Research Institute 2003, SC/F13/SP15).

### Measurements of standard length and weight

Standard lengths (from tip of lower jaw to notch in tail flukes) of common minke whales were measured to the nearest centimeter (cm) in most cases on-board the catcher boats. In the scientific programme a standard morphometry was performed (SC/F13/SP17) including several measurements of girth for bioenergetics studies (SC/F13/SP8, SC/F13/SP10). Foetuses were measured to the nearest cm and weighed to the nearest kilo (kg) or to the nearest gram (g) for the smallest ones.

### 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 g, and their mean size used when pairs were obtained, or single weight used when the other ovary was missing. Uterine cornua was measured on the uterus lying flat on a level surface (working plane or ships deck), to the next 5 millimeters (mm). Mammary gland depth was measured in a standard fashion, to the nearest mm.

*The ovaries* were sliced at 0.5 cm intervals to study the numbers and sizes of corpora, 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)(C. Lockyer 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 the size, except in case of the *Corpus luteum* which was measured in three dimensions and weighed on a scale. Only the largest follicle for each ovary was measured, in two dimensions. Each female was assessed mature or immature from the status of the ovaries. If a *Corpus luteum* or *Corpus albicans* and *Corpus abberance* were present in either of the ovaries, the whale was assumed mature, otherwise immature. Pubertal females

where characterized as having large and many follicles and developing ovaries. Females with *Corpus luteum* were classified pregnant, even if foetus were not found in the uterus. Females with *Corpora albicantia* but no *Corpus luteum* and no foetus were classified as anoestrous – (i.e. mature and “resting”)(Table 2).

*The testes'* histology was studied for sexual maturity. Both testes were weighed after removing the epididymis and a cross section taken midway 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 and one from the central part or core (C) of the testes. The fixated samples were dehydrated, embedded in paraffin, sectioned on a microtome in 6-10 micrometers ( $\mu\text{m}$ ) 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 400 $\times$ , 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 3). 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, see Table 4 (Sigurjónsson et al. 1990; Halldórsson and Víkingsson 2001). Estimation of tubules density or cover was made by counting tubules in cross-sections using 10 $\times$ 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 4 $\times$ 10 magnifications, but sometimes 10 $\times$ 10 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 calculated;  $(C + P)/2$ .

### **Age determination and estimations of parameters of growth in standard length**

Age determination methods are described in SC/F13/SP15. ASP-ages, which were decimal ages, were compared with total number of corpora (*Corpus albicans*, *Corpus luteum* and *Corpus abberance*) in mature females, because from ovarian corpora numbers and transition phase age, the age of mature females have been deducted (Ohsumi 1986). Throughout this paper when referring to age, it is ASP-age (t) unless specified otherwise.

For estimation asymptotic standard length ( $Y_{\infty}$ ), growth constant (K) and theoretical age at zero standard length ( $t_0$ ), for male and female minke whales, four growth-curve models were tried out;

$$\text{Gompert's } [y = Y_{\infty} \times e^{t_0 \times \exp(-K(t))}],$$

$$\text{Logistic } [y = Y_{\infty} (1 + e^{-K(t-t_0)})^{-1}],$$

$$\text{Richard's } [y = Y_{\infty} (1 - e^{-K(t-t_0)})^m],$$

$$\text{Von Bertalanffy } [y = Y_{\infty} (1 - e^{-K(t-t_0)})],$$

### **Statistical analyses**

Sex-ratio was studied using chi-square test, assuming equal proportions of females and males, in foetuses and 0+ animals. Mean body length and age at maturity was estimated for females

and males using Logistic Regression,  $\text{logit}(\pi_i) = \alpha_i + \beta_1x_1 + \beta_2x_2 + \beta_3x_3 + \dots\beta_qx_q$ , incorporating Julian day, months and years of sampling, and in case of the age, standard length and standard length $\times$ age interactions were included. Whales were classified in two groups mature or non-mature (immature and pubertal animals were classified as non-mature other groups as mature). Average age at sexual maturity was also calculated by the method presented by DeMaster (1978). Diameter of follicles, maximum size of *Corpora albicantia*, *Corpora lutea* and *Corpora abberantia*, were regressed against Julian day, month and years of sampling, using a simple linear model, and tested by performing GLM analyses in relation to those terms. The weight of ovaries, were analyzed with GLM in relation to sampling year, standard length of females and maturity stages. The mean size of uterine cornua, was related to maturity stage, standard length of females, sampling day and year. The mammary gland depth was related to maturity stages, sampling years, Julian day and standard length of females, by using GLM too. Trend in size of uterine cornua in relation to day of the year was investigated with linear regression. Mammary gland depth was also investigated in relation to years (as a factor) with ANOVA. The relationship between corpora number and ASP-age was investigated by using resistant regressions and least trimmed squares, 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 GLM. The relationships between mean diameter of seminiferous tubules in testes and age, and Julian day was investigated with GLM. All multiple comparisons were made with the method of Tukey honest significant differences (TukeyHSD). Correlation between weight of testes and the mean diameter of the tubules, and diameter of *Corpora lutea* and standard length of foetuses, was investigated with Spearman Rank correlation coefficient. The relationship between day of the year and foetus weight was tested (with  $\ln$ - $\ln$  transformations, a power relationship assumed) using a Linear Model. The mean-diameter and total number of *Corpus albicans*, weight of testes in relation to ASP-age, weight of ovaries in relation to standard length of females, and the relationship between weight of testes and diameter of the seminiferous tubules, as well as mean diameter of seminiferous tubules in relation to ASP-age, was smoothed with LOESS for creating a trend line. Asymmetry in activity of ovaries was investigated with two sided and paired T-test. Four non-linear models were fitted to the age and standard length data of 0+ animals, the Gompert's, Logistic, Richard's and von Bertalanffy's growth curves. A Nonlinear Model was fitted to the data on, standard length and weight relationship and standard length and day of the year relationship of foetuses, and the relationship between diameter and weight of *Corpus luteum*. Akaike Information Criteria (AIC) was used to decide how well each model fitted the growth data. Statistical analyses were performed with R (R Development Core Team 2010; Verzani 2005; Everitt and Hothorn 2010).

## RESULTS

### Standard length and weight, twin foetuses and sex ratio of minke whales

Most of the sampled minke whales were mature animals (Table 2), and good number of the females pregnant. Female foetus were on average significantly longer than male foetuses, taken into account day of the year and sampling year ( $F_{1,70} = 13.04$ ,  $P = 0.01$ ), average standard length for foetus females and males being 106.0 and 90.7 cm respectively. Average standard lengths for 0+ females and males in the sample were 769.8 and 744.4 cm respectively. Total sex ratio was 107 female and 101 males, for 0+ animals, not significantly different from 1:1. Foetal sex ratio was 27 females and 35 males, not significantly different from 1:1 either. One out of 72 pregnant females had twin foetus (1.4%). The female was 8.70 meters in standard length and 42 years, caught 3 July 2006, which had a 34 cm male and 32 cm long female foetus, in her womb. A nonlinear power relationship was fitted to the available data on standard length and weight of foetuses, for combined sexes (Fig. 2).

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

(RSE=4.095 and degrees of freedom (df) = 33). The power was significantly different from zero (T-value = 12.39,  $P < 0.001$ ), but the intercept was not.

### Ovaries

Weight of ovaries ( $W_{ov}$ ) increased in weight with standard length of females ( $L_f$ ) following a concave smoothed curve (Fig. 3). Mean, (SD) and range, for immature, mature and pregnant females being 47.95 (33.74) and 3.0 – 113.5, 96.03 (58.57) and 13.2 – 206.0 and 145.0 (54.41) and 46.0 – 266.0 g, respectively, significantly different in weight in relation to maturity stages ( $F_{2,85} = 25.74$ ,  $P < 0.001$ ).

There was not found a significant correlation between diameter of *Corpora lutea* and standard length of foetuses. Weight and mean-diameter of *Corpus luteum*, showed a power-curve relationship, intercept = 0.002371 (SE 0.001833) and slope 2.613592 (SE 0.190884) (Fig. 4). The intercept was not but the slope was significantly different from zero, T-value = 13.69,  $P < 0.001$  respectively (RSE = 12.78, df = 54, AIC = 448.29).

Total corpora number (*Corpora albicantia*, *Corpus luteum* and *Corpora abberantia*) were not different between left and right ovaries, the difference was 0.04 (95% CI -0.70 – 0.78) and not significantly different from 0 (T-value = 0.11,  $P = 0.91$ ), a sign of symmetrical activity of ovaries.

### 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),  $F_{94,1494} = 28.97$  and  $P < 0.001$  (Table 5). Seminiferous tubule diameter was on average smaller in immature than mature males. Generally peripheral seminiferous tubules had smaller diameter than tubule from the core, on average 0.011 mm less. These differences were all highly significant ( $p < 0.001$ ). There was a significant correlation between weight of testes and the mean diameter ( $D_{semtub}$ ) of the tubules ( $r_s = 0.80$ ,  $P < 0.001$ ). The relationship was best described by an increasing concave function. Scatter of the data was high and the relationship for mature males was estimated using a smoothed curve (Fig. 5). Immature, pubertal and mature males had mean, (SD), range of weight of testes and diameter of seminiferous tubules, 37.8 (25.08), 7 – 67 g and 57.4 (39.44) 1 – 91.4  $\mu\text{m}$ , 136.7 (16.07) 125 – 155 g and 99.9 (18.44) 73.0 – 129.7  $\mu\text{m}$ , 640.6 (287.11) 123 – 1384 g and 139.1 (29.83) 79.1 – 219.3  $\mu\text{m}$ , respectively. 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 diameter of the seminiferous tubules reached a asymptotic size at 20 years of age and did not change much after that (Fig. 6).

Inspecting the density (or % coverage) of seminiferous tubules in testes, there was observed a highly significant correlation ( $r_s = 0.41$ ,  $P < 0.001$ ) between mean diameter of tubules and the mean density (or cover) of combined cover measurements in peripheral and central parts of the testes (Table 6). The difference between coverage of tubules in central and peripheral samples were significantly different from 0, with mean = 0.35 ( $T$ -value = -0.23,  $P = 0.82$ ). GLM-analyses indicated that there was a significant difference between cover of tubules in peripheral and central parts of testes between immature, pubertal and mature males ( $F_{6,74} = 5.56$ ,  $P = 0.01$ ) and between mature and immature males ( $P = 0.01$ ). There were not significant differences in combined cover, between maturity stages of males and not a significant trend with years of sampling.

### Growth of foetus and 0+ animals

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

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

( $\text{RSE} = 29.76$ ,  $\text{df} = 70$  and  $\text{AIC} = 696.91$ ), increasing from about 30 cm in total standard length in April to about 1.57 meter in September (Fig. 7). Natural logarithms of foetus weight ( $\ln F_w$ ) increased significantly with natural logarithms of day ( $\ln D$ ) ( $T$ -value = 4.79,  $P < 0.001$ ). A curve linear relationship could not be fitted, however the linear  $\ln$ - $\ln$  relationship;

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

described this significantly ( $R_{\text{ad}}^2 = 0.36$ ,  $F_{1,29} = 17.91$ ,  $P < 0.001$ ), with both intercept and slope significant ( $T$ -values and  $P$  were -5.65,  $< 0.001$  and 6.02,  $< 0.001$  respectively), implying that a power curve-linear relationship existed. According to the established standard length-weight relationship of foetus (Fig. 1) a 30 cm and 157 cm long foetus would have body weight of 0.4 and 82 kg respectively, growing in weight nearly 82 kg in 6 months.

Parameters for growth curves for 0+ animals are presented in Table 7. Of the growth models tested, von Bertalanffy gave the best fit and lowest AIC-values, both for females and males (Fig. 8 and 9). The Gompert's and Logistic growth models did nearly as well as the von Bertalanffy model, but 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. Using the female von Bertalanffy growth-model to calculate standard length at age zero (calf standard length at birth), gave 191 cm, see Fig. 7 for comparison with collected data on foetus size.

For females, the mean standard length and age of immature, pubertal, mature, anoestrous and pregnant animals and for males mean standard length and age of immature, pubertal and mature, are given in Table 8.

### Foetuses, ovaries, weight and number of ovarian bodies

The sexual maturity of 84 females of 107 could be determined by the presence of one or more corpus in either of the ovaries, revealing 80.4% of the sample sexually mature and 18.6% immature (Table 2). The frequency distribution of the total numbers of *Corpus luteum*,



*Corpora abberantia* and *Corpora albicantia* in both ovaries is shown in Fig. 10. Total of 45 (60.8 % of the sample) mature females with both ovaries collected had less than 10 corpora of this type, whereas 7 (9.5%) animals had in excess of 20. The highest number of such corpora in a pair of ovaries was 42.

Diameters of ovarian bodies were different between types of bodies and maturity stages of females. Corpora were largest in pregnant females and follicles were smallest in immature females in general (Fig. 11). Further investigation showed that neither maximum follicle diameter nor *Corpus luteum* diameter showed significant trend with Julian day and year. Maximum size of *Corpus albicans* was also not significantly different between days of the year or sampling years. Diameter of *Corpora albicantia* ( $D_{ca}$ ) declined with total number of *Corpus albicans* (Fig. 12), underlining the fact that *Corpora albicantia* do not disappear, instead reach a minimum size 5 - 10 mm, and form permanent scars in the ovaries.

In the total sample 82 females which had active *Corpus luteum*, i.e. *Corpus luteum* of pregnancy or ovulation, 57.1 % (48) had foetus collected from their womb. Seven sexually "matured" females had only *Corpora albicantia* in the ovaries was neither pregnant nor ovulating (anoestrous), so about 91 % of mature females were reproducing, which could mean they give birth each 1.1 year. A total of 72 females had foetus recorded or collected and one female (1.4%) twin foetus, as mentioned above.

### ***Mammary gland***

Mammary gland depth was greatly hypertrophied in mature females (mean 41.8 and range 22.0 – 80.0 mm). The difference in gland depth was generally adequate to distinguish between mature and immature females, significant ( $P = 0.006$ ). However, differences between immature (mean 15.1 and range 2.0 – 55.0 mm) and pregnant females (mean 26.0 and range 10.0 – 90.0 mm), were not statistically significant ( $P = 0.10$ ). No significant time trends were observed in mammary gland depth.

### ***Uterine cornua***

There was not observed a significant difference between left and right uterine cornua. Uterine cornua increased in size at maturity, and varied in width from on average 40.5 mm in immature to 194.1 mm in pregnant females. the smallest for pregnant females was 35.5 mm, the largest for immature females was 46.5 mm and anestrous females, had uterine cornua in the range of 57.5 – 95.0 mm. There was a significant difference in uterine cornua size between pregnant and immature females ( $p = 0.0003$ ), and size of uterine cornua showed a significant ( $p = 0.02$ ) increasing trend with day of the year for pregnant females (Fig. 13) (AIC = 335.18).

### **Standard length at maturity**

Results from the GLM analyses indicated that time of sampling did not influence the onset of maturity of females, however, standard length (L) of females did ( $Z = 4.05$ ,  $P < 0.001$ ). The model being;

$$\text{Logit}(\pi_i) = -19.416(\text{SE } 5.157) + 0.028(\text{SE } 0.007)L$$

where  $\text{logit}^2(\pi_i) = \ln(\pi_i/(1 - \pi_i))$  (Residual Deviance = 50.76,  $df = 99$ , AIC = 54.76), which indicated that the total standard length at which 50% of females was mature was equal to 713 cm ( $\pm 15$ cm). In the catch the longest immature female was 774, the shortest mature female was 682 cm (Table 8). Similarly the results from the GLM analyses indicated that Julian Day and year of sampling did not influence the onset of sexual maturity of males, but the standard length (L) of males did so significantly ( $Z = 3.20$ ,  $P = 0.001$ ). The model being;

<sup>2</sup> The logit of a probability is the log of the odds of the response taking the value one (Everitt and Hothorn 2010).

$$\text{Logit}(\pi_i) = -14.284(\text{SE } 4.086) + 0.023(\text{SE } 0.006)L$$

(Residual Deviance = 47.06, df = 100, AIC = 51.06), which indicated that the standard length at which 50% of males was mature was equal to 639 cm (32 cm). The standard length range for pubertal males was 603 – 764 and the shortest mature male was 566 cm (Table 8).

### Age at maturity

Age at maturity of females was estimated with the method of DeMaster (1978) as being at 10.4 years of age (95% CI 9.9 – 11.0 years), the same mean age at maturity that was estimated with a logistic regression, which had much wider 95% CI; 2.9 – 35.7 years. The fit was significant for age ( $P = 0.0001$ ) and the intercept was also significant ( $P = 0.002$ ). Results from an ordinary linear regression of ASP-age and total number of ovarian corpora (that is *Corpora albicantia*, *Corpora lutea* and *Coprora abberantia*), indicated that age of maturity was 9.4 (SE 0.690) and that each year 0.84 (SE 0.053) corpora were formed, that is to say 1.2 (95% CI 1.1 – 1.4) years go between a corpus formation, both intercept and slope was significantly different from zero ( $P < 0.001$ ). Results from of resistant regression on ASP-age and total number of ovarian corpora, indicated that females became mature 8.7 years old and produce 0.94 corpora annually, or there was just about 1.1 years between ovulations. However, results from the least-trimmed squares indicated mean age of maturity at 10.3 years and 0.74 corpora being formed yearly (Fig. 14). The youngest mature female caught was 11.2, the oldest immature female was 12.3 and the only pubertal female was 12.8 years of age (Table 8).

Age at maturity of males could not be estimated with the method of DeMaster (1978) due to imbalanced data, and a logistic regression of age on whether mature or not, gave a significant fit (the intercept was not but the slope was significant at the 1% level), with  $A_m = 6.6$  years (95% CI 1.9 – 38.8). The youngest mature male was 6.1 and the youngest of the seven pubertal males caught was 8.1 years of age (Table 8). Testes weight was not found to be significantly different in relation to years of sampling, day of the year and standard length of animals. Their mean weight was much higher in mature males than in pubertal and immature males 744.25g, 167.50g and 35.33g respectively (Fig. 15). Maximum weight of single testes in immature, pubertal and mature males was 67, 260 and 1362 g respectively, and minimum weight of single testes in mature males was 337 g. Males with immature testes were all less than 14 years old. The youngest males with mature testes weight were, 6 years. Males of age 20 – 30 years were observed to have testes with the highest weight (Fig. 15).

### Seasonality of reproduction

#### Females

Mean size of uterine cornua showed a significant ( $p = 0.02$ ) increasing trend with day of the year, in pregnant females, less or not at all in immature and anestrus females (Fig. 13) Ovarian weight was not significantly different between years, months or days, maturity stages taken into account.

Further investigation showed that neither maximum follicle diameter nor *Corpus luteum* diameter showed significant trend with Julian day and year.

#### Males

Results from GLM indicated that diameter of seminiferous tubules varied significantly with day of the year (T-value = 6.29,  $P < 0.001$ ). The diameter increased linearly from May to September, on average about 0.49 (SE = 0.08)  $\mu\text{m}$  each day. This was however significantly different between immature, pubertal and mature males (Fig. 16). 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 and pubertal males. There were also observed a significant positive trend

between cover of seminiferous tubules in testes and Julian day ( $P = 0.02$ ), with estimated increase about 0.1% (SE = 0.04) per day (Fig. 17), even though the variability in the data was great.

## DISCUSSION

### Sampling and whaling operations

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 may occur throughout the year. The breeding grounds of common minke whales are unknown, although satellite tracking has indicated a link between Icelandic and western African waters (SC/F13/SP18). Lactating females with calf are a rare sight in Icelandic waters indicating that most calves are weaned before entering the Icelandic feeding grounds in the spring. Although no size restriction were imposed in the study, and whales were randomly selected, no animals less than 461cm were taken or observed.

### Age determination, onset of maturity and the transition phase

Ageing of minke whales was not based on reading GLG's from ear-plugs or *Tymphanic bulla*es 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* or ear-plugs has neither given satisfactory results, nor as good results as for the fin whale (Lockyer et al. 1977) and sei whale (Lockyer 1972). Making assumption on age at sexual maturity and ovulation rate, age-determination (A) of mature females can be derived from the formula;

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

where O was the ovarian corpora numbers in the combined left and right ovaries. Similar equation has been used by other whale researchers (Lockyer 1972). This method can not be used to age immature females and males of all ages, 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 (see Marine Research Institute 2003). This aging method met the criteria for routine ageing of harvested whale stocks. It yields accurate assessment of age, offers repeatability and was not too laborious.

Horwood (1990) reported an annual ovulation rate as 1.0 to 1.1, using corpora and bulla ages and corpora and ear plug ages respectively, which was similar to that observed in this study using corpora and ASP-ages. Our results, 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 9 - 10 years.

### Female reproduction

In the present study about 91% of the mature females were determined pregnant from inspection of ovaries and the uterus. In an earlier Icelandic study based on commercial catches (Sigurjónsson et al. 1990) foetuses were detected in about 80% of mature females. However, foetuses are easily overlooked in the traditional processing by whalers, and in a smaller sample examined by scientists the apparent pregnancy rate was determined as 94% (Sigurjónsson et al. 1990). This is similar to the results of the present study and also to results from 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 1974 and 1981), and W-Greenland 89% (Larsen 1984).

Logistic regression results indicated that the standard length at which 50% of females was mature was equal to 713 cm, which is similar to that observed for the minke whale females in the Barents- and Norwegian Sea, being 7.2 meters (Stenseth et al. 1993), Kjeld et al. 2004).. Jóhann Sigurjónsson et al. (1990) observed 7-7.5 m total standard 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), 750 cm off W-Greenland and 737 cm from Newfoundland material (Larsen 1984; Mitchell and Kozicki 1975). The present results are also within this range.

In the present study the regressions of ASP-age with total number of corpora gave age at maturity about 9 – 10 years. The method of DeMaster (1978) gave similar results; however, the number of samples in each age-group was much less than the 25 recommended as minimum in his paper. Age-at-maturity of around 10 years is considerably higher than reported in most earlier studies (Christensen 1981; Mitchell & Kozicki 1975). In his review, Horwood (1990) reported age at maturity as 6-7 years and in a previous Icelandic study the value was estimated as 5-6 years (Sigurjónsson et al. 1990). While an increase in age at sexual maturity in recent decades cannot be ruled out, the difference between the present and earlier studies is not statistically significant and may be related to different methods of age determination in addition to low sample sizes.

One female out of 72 (1.4%) had a twin foetus. This is rarely observed in baleen whales and cetaceans in general. According to Horwood (1990) multiple foetuses have been found in 0.6% of analysed minke whales. It is generally considered that even twins were unlikely to go to term and no certain twins have been observed free-living in the oceans.

There were not found any evidence for asymmetrical activity of ovaries in the common minke whale females in Icelandic waters, as found for the Icelandic harbour porpoises (*Phocoena phocoena*) females, where the left ovary was dominating in activity (Halldórsson and Víkingsson 2001). In minke whale females rather limited studies indicate that each ovary contributes equally and they tend to ovulate alternatively (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 reliable means of determining the sexual status of the animals (Table 4).

Estimation of length at sexual maturity was severely hampered by low sample sizes. Logistic regression results indicated that the total standard length at which 50% of males was mature was equal to 639.0 cm. This is somewhat shorter than the 675 cm reported by Stenseth et al. (1993), for the minke whale males from the Barents- and Norwegian Sea and Kjeld et al. (2004) from N-Atlantic, but not far from the values Horwood (1990) gives in his table 7.1, for males. The standard length range for pubertal males was 6.0 – 7.6 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, also higher than observed by (Jonsgaard 1951; Christensen 1981), but Sigurjónsson mentions that criteria for maturity were somewhat different, than used by Christensen (1981) and Jonsgaard (1951). None of the above differences between the present and previous studies were statistically significant.

Using weight of testes as criteria for maturity (Fig. 15) indicates, that all immature males were less than 14.3 years of age, pubertal males were 8-17 (with one 38 years of age as an outlier), and the youngest mature males of age 6.1 (Table 7), or similar as reported by Stenseth et al. (1993), for the minke whale males from the Barents- and Norwegian Sea. Results from a marginally significant (5%) logistic regression of maturity on age indicated  $A_m$  as about 6 years.

The weight of testes reached a maximum just after the 20<sup>th</sup> 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 (SC/F13/SP14). Another cause for the variability in size of testes, diameter and cover of seminiferous tubules, could be individualistic quiescent in sexual activity of males captured at the same site and date, as Neuenhagen et al. (2007) observed in males of white-sided dolphin (*Lagenorhynchus acutus*) in the northeastern Atlantic.

### **Growth, asymptotic standard length and other factors of morphological importance - comparison of the Icelandic common minke whale with other minke whale populations.**

The value of the power constant (2.8) in the standard 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 (Horwood 1990). The slope of a curve linear relationship for growth in foetus in standard length was quite similar to those presented in (Horwood 1990) also, even if months was the time frame, not days as here. A curve linear relationship for the growth of foetus in weight could not be established due to low sample size. 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 standard length-weight relationship for foetus presented in this paper. Standard length at birth was estimated with the von Bertalanffy growth model as about 2 meters. Víkingsson (2004) estimated that calves of common minke whales were 2.5 – 2.8 meters and 150 – 300 kg at parturition. .

Jongsgaard (1951) considered the maximum average standard length 8.2 m for males and 8.8 m for females, which was more similar to the values from Icelandic waters. Maximum standard 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  $L_\infty = 8.33$  and 9.07 meters,  $K = 0.169$  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 they turned out more similar after the modifications Christensen made by drawing by eye, Fig. 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  $L_\infty = 7.6$  m,  $K = 0.25$  per year, and  $t_0 = -3.2$  years. Shorter asymptotic standard length, but similar  $K$  and  $t_0$  as for the minke whale females from Icelandic waters, probably because of a lack of older females in the Newfoundland sample (Horwood 1990). From catches off Japan, Omura and Sakiura (1956) reported maximum standard 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).

### **Seasonal changes in reproduction**

The female reproductive data did not show any seasonal differences in values, except for foetus growth of course. The intercept of the foetus standard length growth-curve indicated that zero standard length was at day one of the year. Likewise, foetus reaches birth-standard 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 standard length and weight indicates large variability in dates of conception as has also been shown for other baleen whales (C. Lockyer & Sigurjónsson 1991).

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 common minke whale males caught 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 (Víkingsson 2004).

#### **ACKNOWLEDGEMENT**

The whaling boats and their skippers were w/w Halldór Sigurðsson ÍS-14 skipper Konráð Eggertsson, w/w Njörður KÓ-7 skipper Guðmundur Haraldsson, w/w Trausti ÍS-111 skipper Gunnlaugur Konráðsson, w/w Dröfn RE-35 skipper Gunnar Jóhannsson and w/w Sigurbjörg ST-55 skipper Gunnar Jóhannsson. Apart from the authors (excluding Erlingur Hauksson), the sampling team from the Marine Research Institute included Birgir Stefánsson, Anton Galan (deceased), Inga Fanney Egilsdóttir, Magnús Örn Stefánsson, Þorvaldur Gunnlaugsson, Davíð Gislason, Anna K. Daníelsdóttir, Valerie Chosson-P, Björn Þorgilsson, Einar Jörundsson, Vilhjálmur Svansson. All these people are thanked for their important contributions to the project.

## TABLES

**Table 1. Biological material from common minke whales (*Balaenoptera acutorostrata*) caught off Iceland, in the period 2003-2009. The special permit period lasted 2003 – 2007, with some commercial catch in years 2006 (1 animal) and 2007 (6 animals) and only commercial catch in years 2008 and 2009**

Year	Sex organs		Eye pairs aged (sampled)	Foetus	Animals collected for science		
	Testis	Ovaries			Females	Males	Total
2003	22	13	26 (33)	9	13	23	36
2004	11	15	24 (24)	10	15	11	26
2005	18	14	33 (33)	7	14	20	34
2006	29	28	58 (60)	19	28	31	59
2007	9	25	34 (37)	14	27	15	42
2008	0	0	0 (0)	1	1	0	1
2009	1	1	0 <sup>3</sup> (15)	9	9	1	10
<b>Total</b>	<b>88</b>	<b>96<sup>4</sup></b>	<b>175 (202)<sup>5</sup></b>	<b>69</b>	<b>107</b>	<b>101</b>	<b>208</b>

**Table 2. Reproductive status of female and male common minke whales (*Balaenoptera acutorostrata*) sampled in Icelandic waters, in 2003-2009**

	Females (n)	Males (n)
Immature	18.63% (19)	4.60% (4)
Pubertal	0.98% (1)	8.05% (7)
Mature	80.39% (82 <sup>6</sup> )	87.36% (76)
	Anoestrous	8.86% (7)
	Pregnant	91.14% (72)
<b>Total</b>	<b>100.00% (102)</b>	<b>100.00% (87)</b>
Inconclusive	5	14

<sup>3</sup> Have not been aged yet

<sup>4</sup> 74 ovaries pairs and 22 females with a single ovary, left or right

<sup>5</sup> Eye lenses from total of 12 animals were unusable for aspartic acid racemisation chemical analyses. Eyes pairs collected from animals in the period 2003-2007 totally 187. Totally were 197 animals obtained for scientific research in that period.

<sup>6</sup> Two of these 82 females could not be classified beyond mature (i.e. pregnant or anestrus).

**Table 3. Maturity stages of testes, by description, in male common minke whales (*Balaenoptera acutorostrata*)**

<b>Stage</b>	<b>Description</b>
<b>Immature</b>	<b>Very small tubules, few large cells with dark stained large nuclei filling the tubular lumen</b>
<b>Maturing or pubertal</b>	<b>Both immature and mature tubules can be found in the samples. Only few cells of either types could be found in some cases</b>
<b>Mature</b>	<b>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</b>
<b>Actively mature</b>	<b>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</b>

**Table 4. Assessment of maturity status of male common minke whales (*Balaenoptera acutorostrata*) based on combinations of maturity assessments of peripheral (P) and central (C) testis tissue samples (final classification)**

Maturity of sample P:	Maturity of sample C:		
	Immature	Pubertal	Mature
Immature	Immature	Pubertal	Pubertal
Pubertal	Immature	Pubertal	Mature
Mature	Pubertal	Pubertal	Mature



**Table 5. 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 common minke whale (*Balaenoptera acutorostrata*) males testes**

Sample location	Maturity	Grand mean	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	0.100	0.048	0.196	0.033	110
	Mature	0.138	0.036	0.292	0.037	640
Total P		0.130	0.036	0.292	0.040	780
C	Immature	0.123	0.095	0.143	0.016	10
	Pubertal	0.073	0.069	0.092	0.007	10
	Mature	0.146	0.060	0.405	0.037	739
Total C		0.145	0.060	0.405	0.038	759
P-C	Immature	0.076	0.051	0.143	0.023	60
	Pubertal	0.100	0.048	0.209	0.035	140
	Mature	0.142	0.036	0.405	0.038	1389

**Table 6. Density (cover) of seminiferous tubules in testes of male common minke whales (*Balaenoptera acutorostrata*), collected in the period 2003-2009, in Icelandic waters**

	Immature (mean (SD) N)	Pubertal (mean (SD) N)	Mature (mean (SD) N)	Total (mean (SD) N)
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

**Table 7. Parameters of the growth curves (SE) for common minke whales (*Balaenoptera acutorostrata*), in Icelandic waters. The model with the lowest AIC value fits the data best**

Growth curve model	Asymptotic standard length ( $L_{\infty}$ )	Growth constant (K)	Theoretical age of zero standard length ( $t_0$ )	Fourth fitting parameter in the model (m)	Akaike Information Criteria (AIC)
Gompert's	Females 838.4 (11.435) <sup>***</sup>	Females 0.186 (0.026) <sup>***</sup>	Females -1.07 (0.198) <sup>***</sup>	None	Females 892.78 Males 891.40
	Males 795.0 (13.427) <sup>***</sup>	Males 0.126 (0.030) <sup>***</sup>	Males -0.54 (0.118) <sup>***</sup>		
Logistic	Females 835.5 (10.810) <sup>***</sup>	Females 0.211 (0.029) <sup>***</sup>	Females 1.85 (0.826) <sup>*</sup>	None	Females 893.07 Males 892.16
	Males 794.8 (13.375) <sup>***</sup>	Males 0.132 (0.031) <sup>***</sup>	Males -3.61 (2.58) <sup>ns</sup>		
Richard's	Females 841.8 (16.239) <sup>***</sup>	Females 0.1624 (0.068) <sup>*</sup>	Females -1.96 (11.204) <sup>ns</sup>	Females 1.092 (2.984) <sup>ns</sup> Males (no fit)	Females 894.67 Males (no fit)
	Males (no fit)	Males (no fit)	Males (no fit)		
Von Bertalanffy's	Females 842.2 (12.304) <sup>***</sup>	Females 0.160 (0.023) <sup>***</sup>	Females -1.61 (1.146) <sup>ns</sup>	None	Females 892.67 Males 890.53
	Males 795.2 (13.476) <sup>***</sup>	Males 0.119 (0.028) <sup>***</sup>	Males -6.41 (3.034) <sup>*</sup>		

**Table 8. Comparison of mean standard length, mean age and ranges of immature, pubertal and mature male and female common minke whale (*Balaenoptera acutorostrata*), with information about pregnancy of females, from the whaling in 2003-2009**

<b>FEMALES</b>									
	<b>Immature</b>			<b>Anestrus</b>			<b>Pregnant</b>		
	<b>Mean</b>	<b>N</b>	<b>Range</b>	<b>Mean</b>	<b>N</b>	<b>Range</b>	<b>Mean</b>	<b>N</b>	<b>Range</b>
<b>Age (yr)</b>	8.7	18	3.4 – 12.3	20.7	9	11.2 – 41.7	19.6	52	10.0 – 39.9
<b>Standard length (cm)</b>	643	19	461 – 774	798	9	730 – 872	800	71	682 - 900

<b>MALES</b>									
	<b>Immature</b>			<b>Anestrus</b>			<b>Pregnant</b>		
	<b>Mean</b>	<b>N</b>	<b>Range</b>	<b>Mean</b>	<b>N</b>	<b>Range</b>	<b>Mean</b>	<b>N</b>	<b>Range</b>
<b>Age (yr)</b>	9.6	4	3.6 – 14.3	13.0	5	8.1 – 16.7	22.0	75	6.1 – 47.4
<b>Standard length (cm)</b>	557	5	482 – 706	688	7	603 – 764	755.9	90	566 - 870

## FIGURES

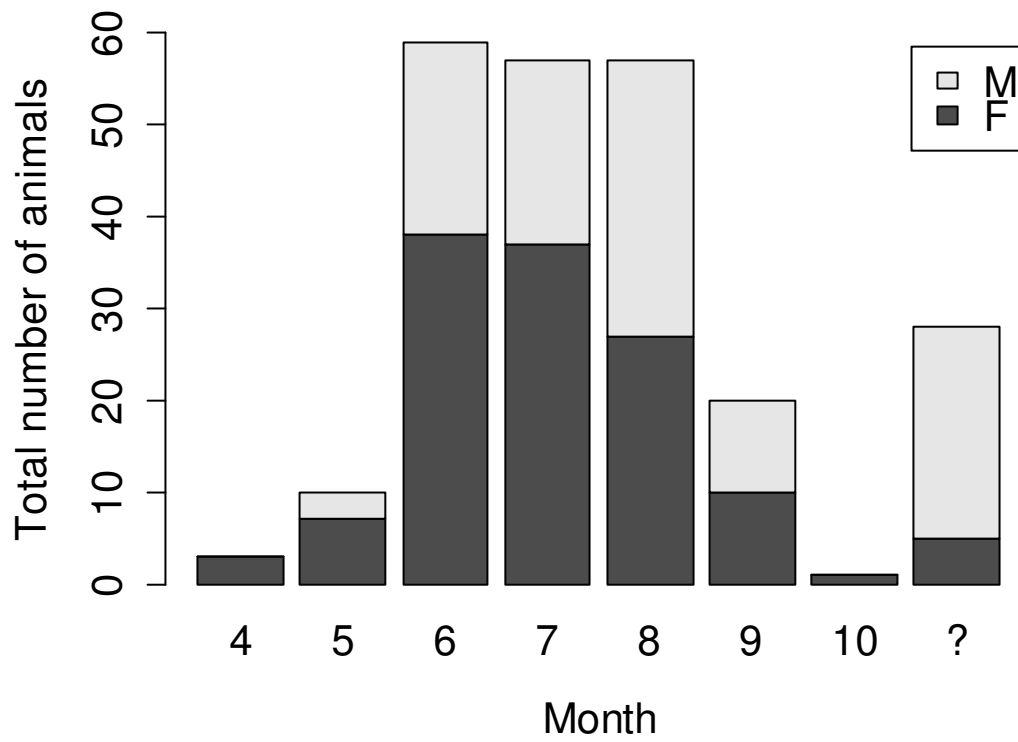


Fig. 1. Number of female (F) and male (M) common minke whales (*Balaenoptera acutorostrata*) sampled by months, during 2003-2009

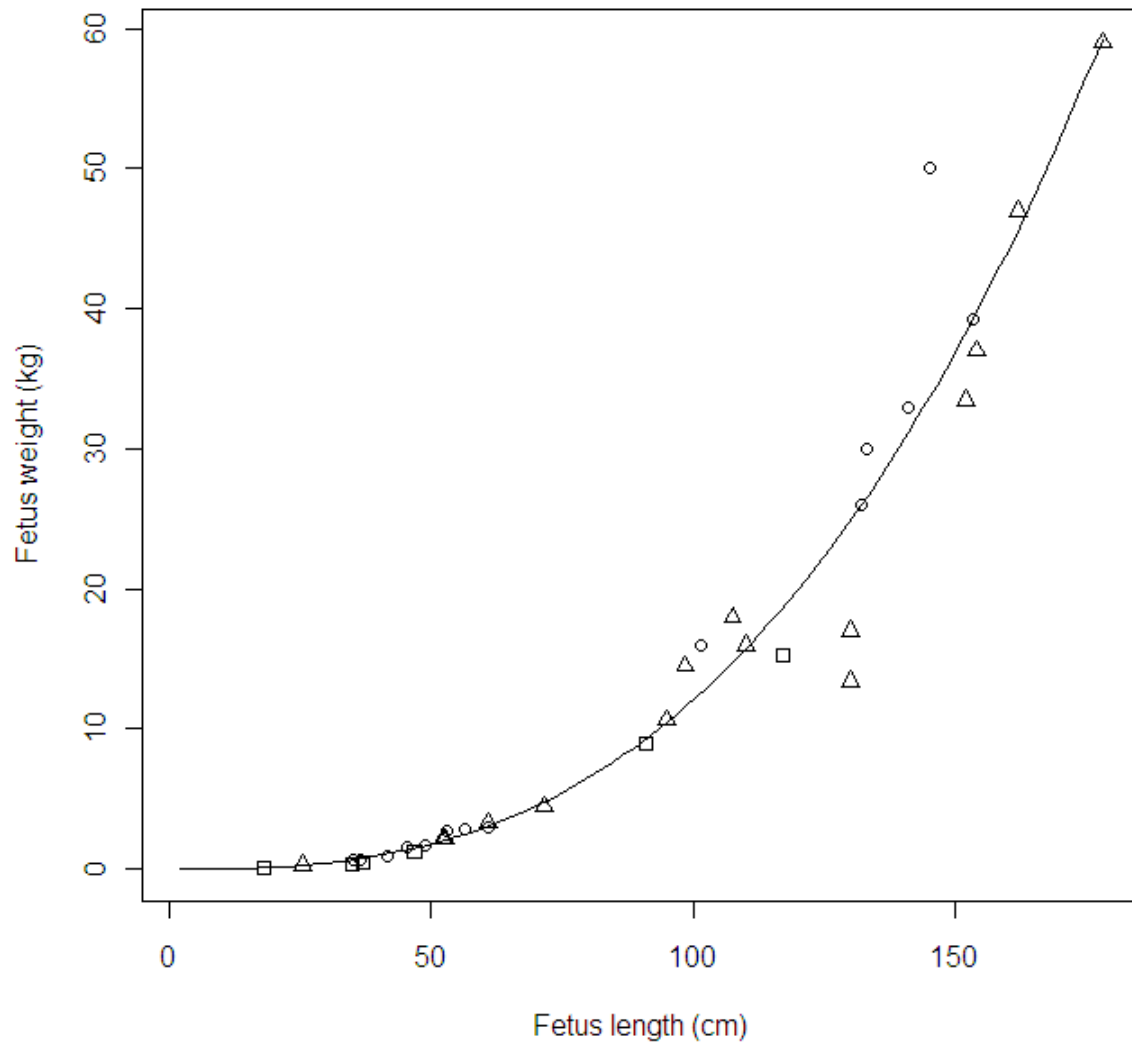
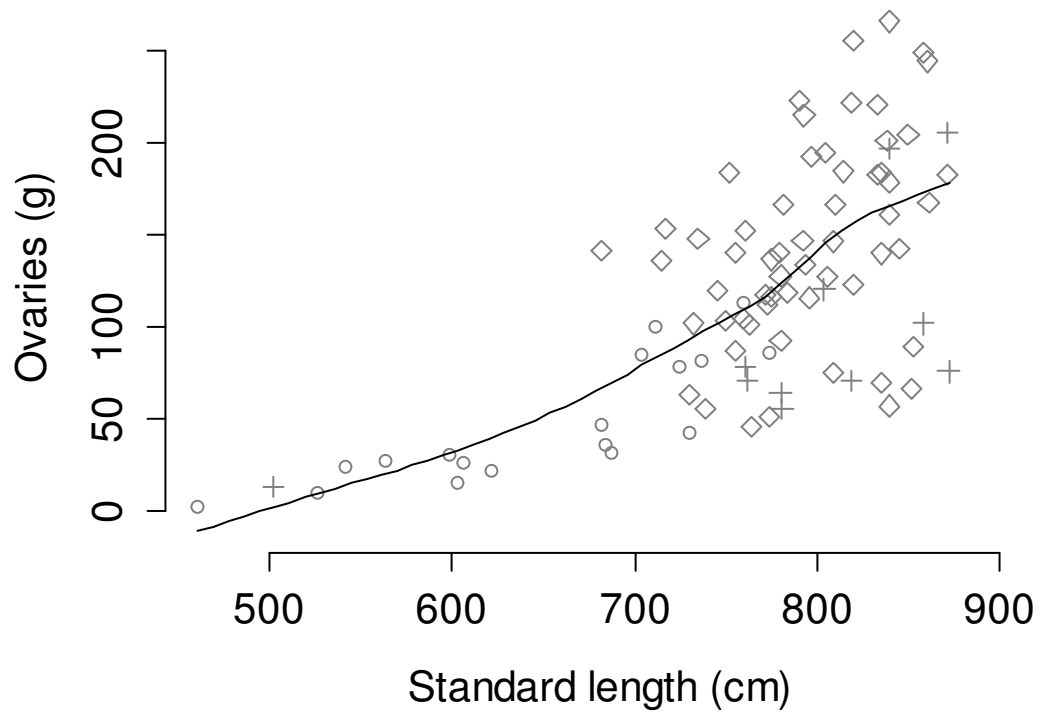
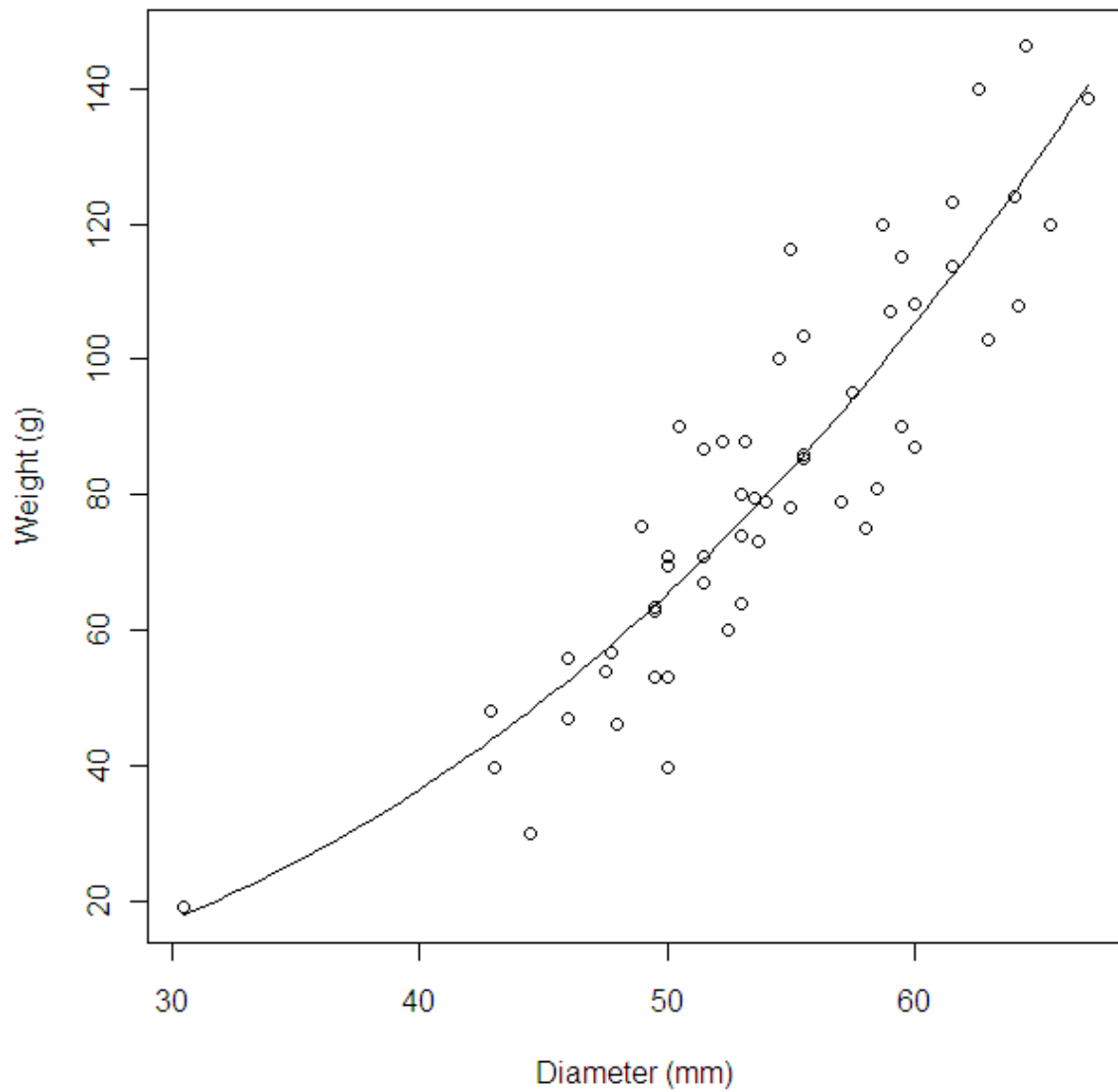


Fig. 2. Foetus weight on standard length for common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters, in the period 2003-2009, ( $\Delta$ ) males, (o) females and  $\square$  sex unknown.



**Fig. 3. Smoothed linear relationship between weight of ovaries (g) and standard length of female common minke whales (cm) (*Balaenoptera acutorostrata*), (o) immature, (+) mature and (◇) pregnant.**



**Fig. 4.** A power relationship, between weight of and mean diameter of *Corpus luteum* in ovaries of female common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters in the period 2003-2009.

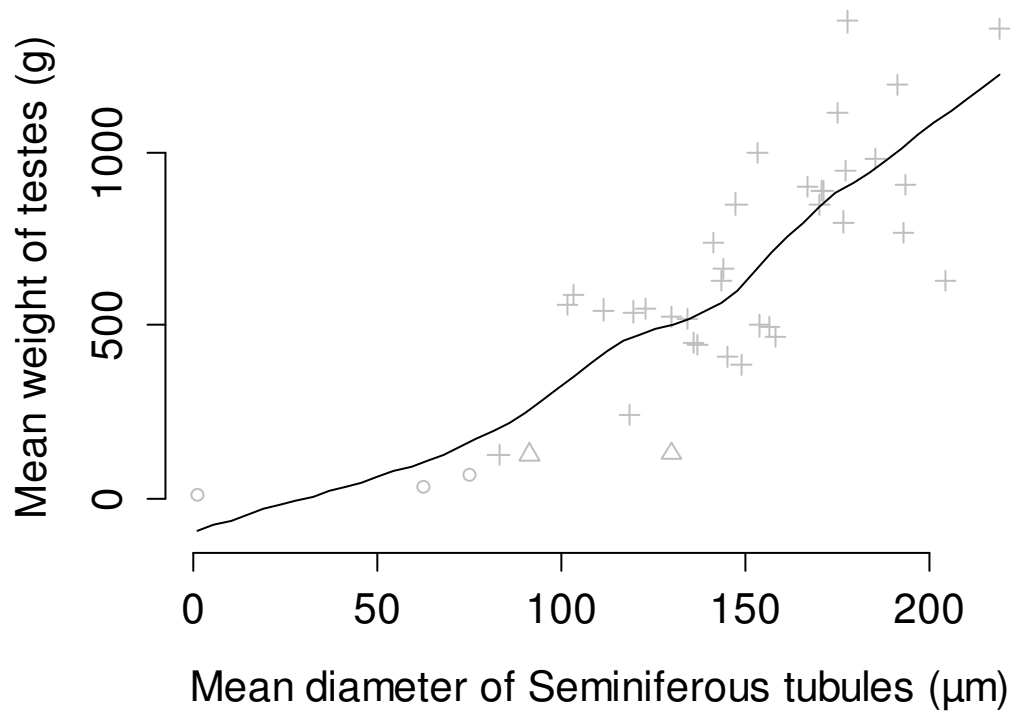


Fig. 5. A smoothed concave relationship, between mean seminiferous tubule and mean weight of testes in common minke whale (*Balaenoptera acutorostrata*) males, caught in Icelandic waters in 2003-2009, (o) immature, (Δ) pubertal and (+) mature males.



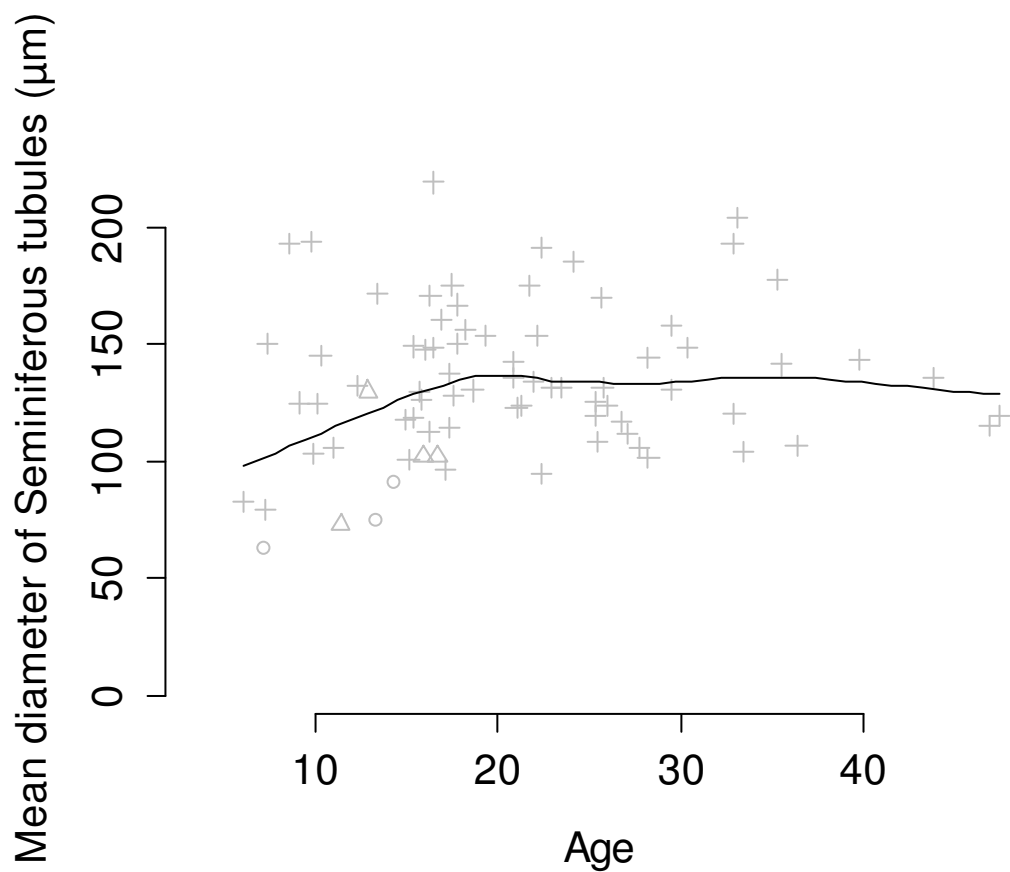
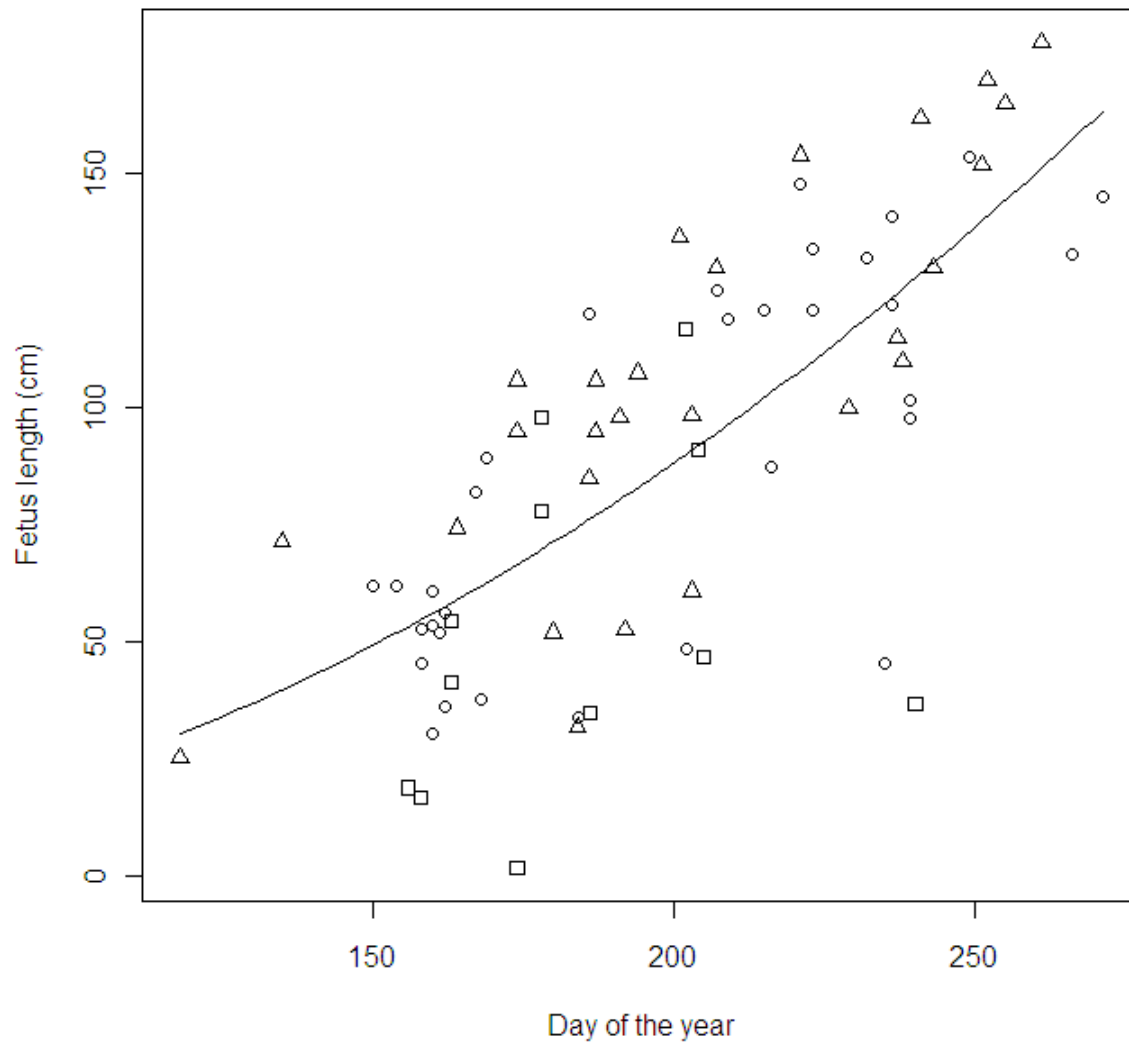


Fig. 6. Mean diameter of seminiferous tubules in testes in relation to ASP-age, from; (o) immature, (Δ) pubertal and (+) mature common minke whale (*Balaenoptera acutorostrata*) males, caught in Icelandic waters in 2003-2009.



**Fig. 7.** Curve-linear relationship between day of the year (1-365) and common minke whales (*Balaenoptera acutorostrata*) foetus standard length, (□) sex unknown, (Δ) males and (o) females, from female common minke whales caught in Icelandic waters in 2003-2009.

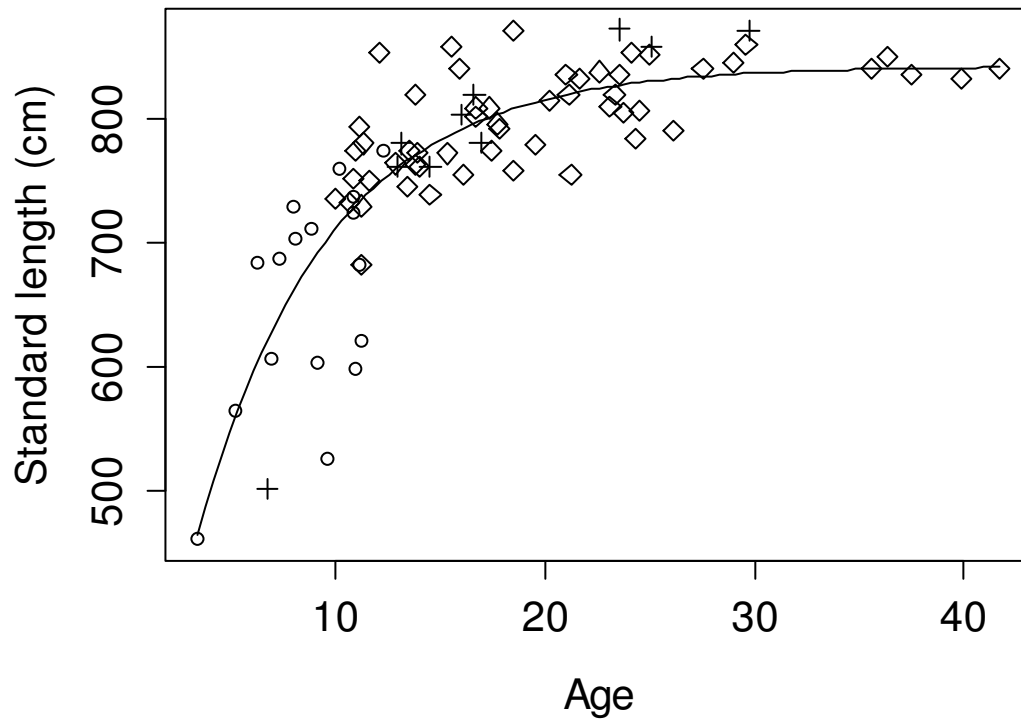


Fig. 8. Standard length with ASP-age in female common minke whales (*Balaenoptera acutorostrata*) from Icelandic waters, caught in the period 2003-2009, (o) immatures, (+) mature and (◇) pregnant females, with von Bertalanffy fitted curve..

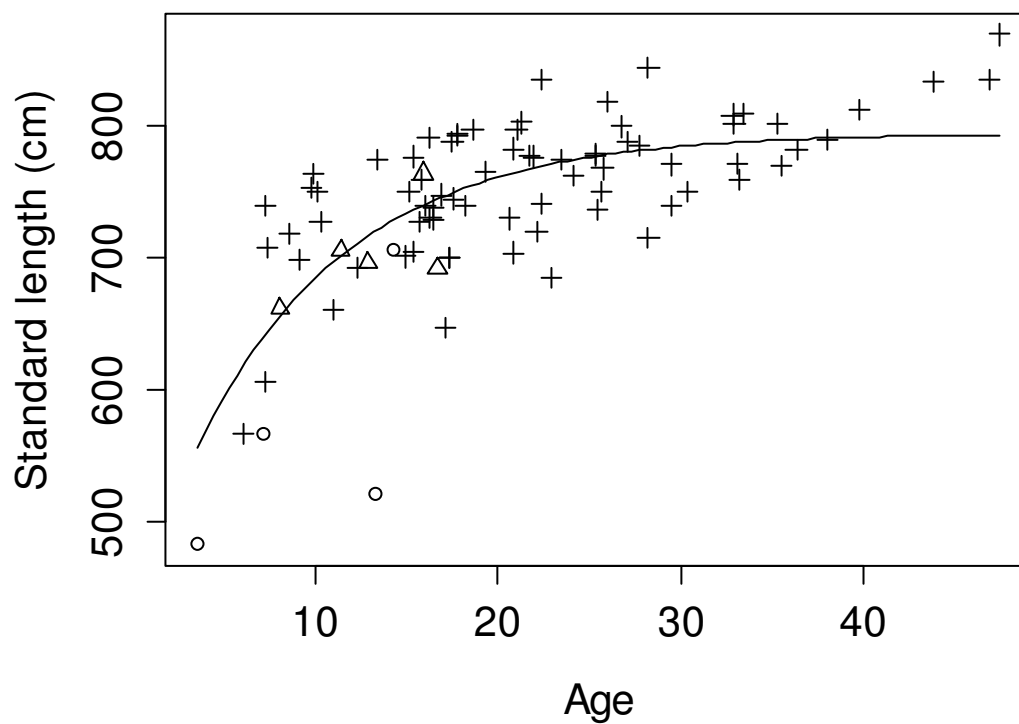
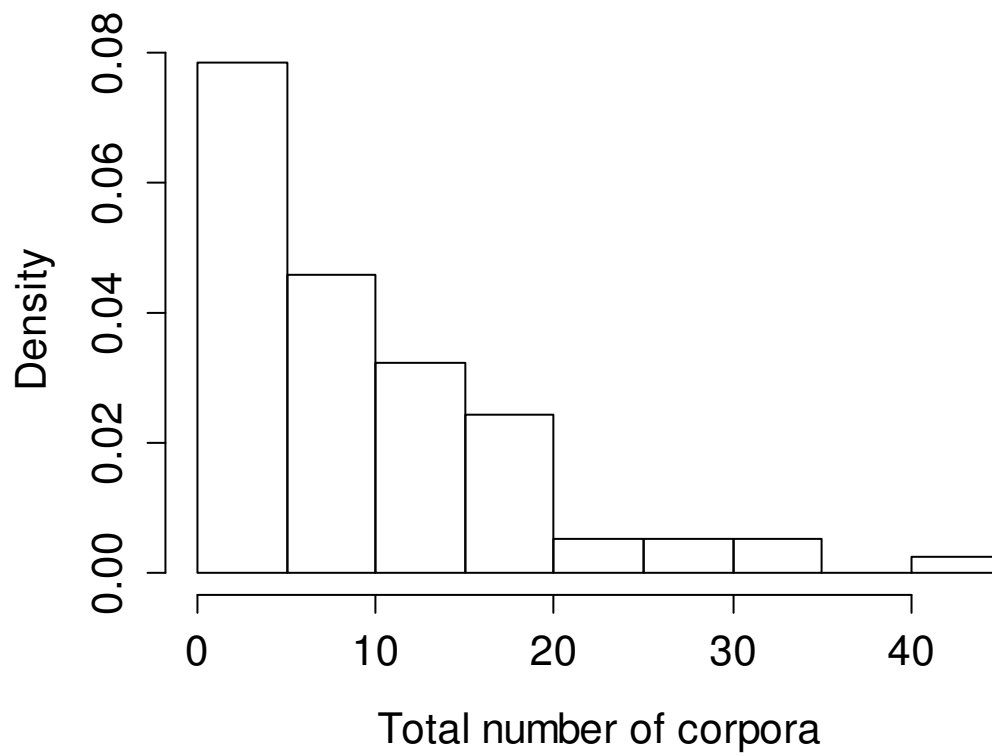
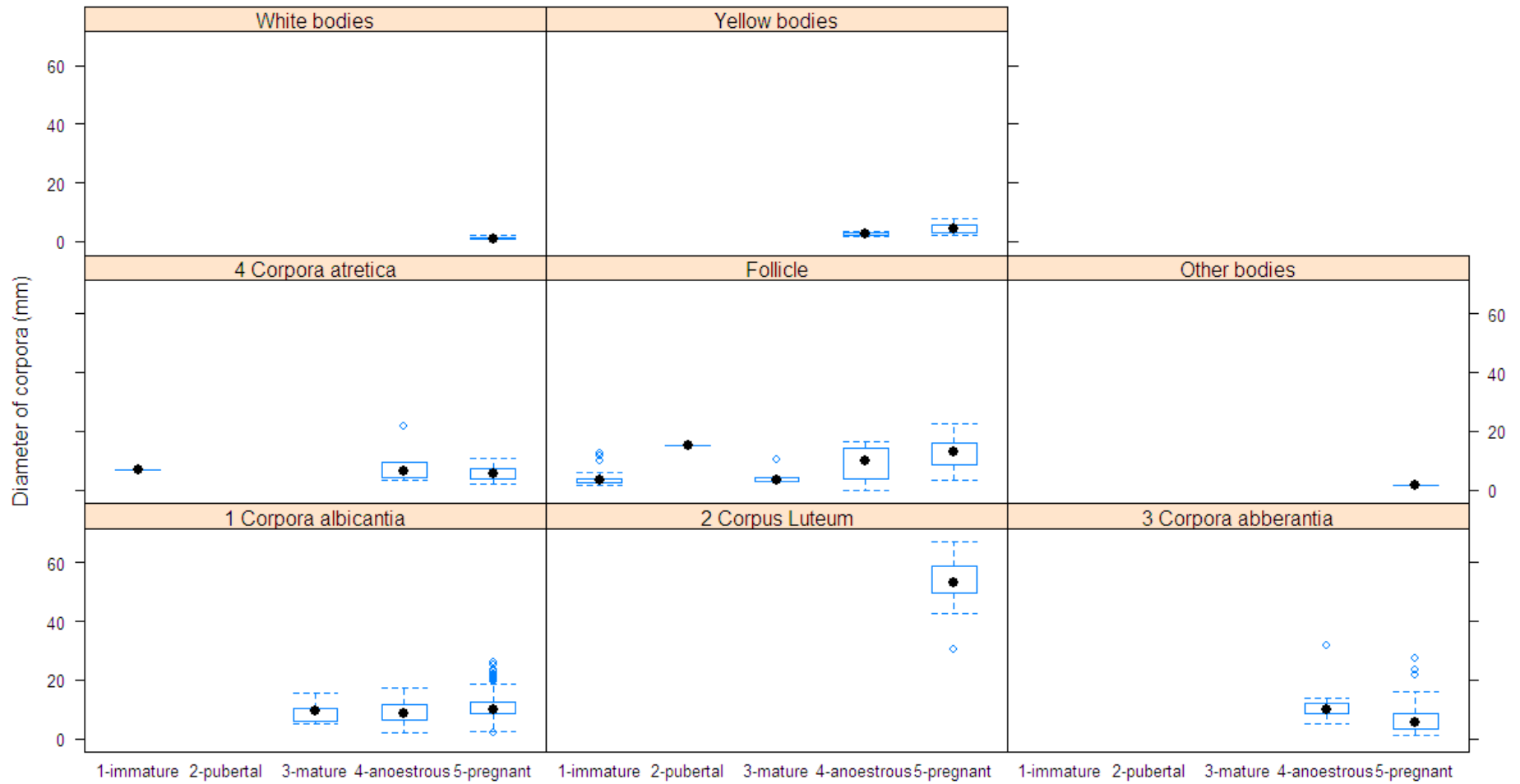


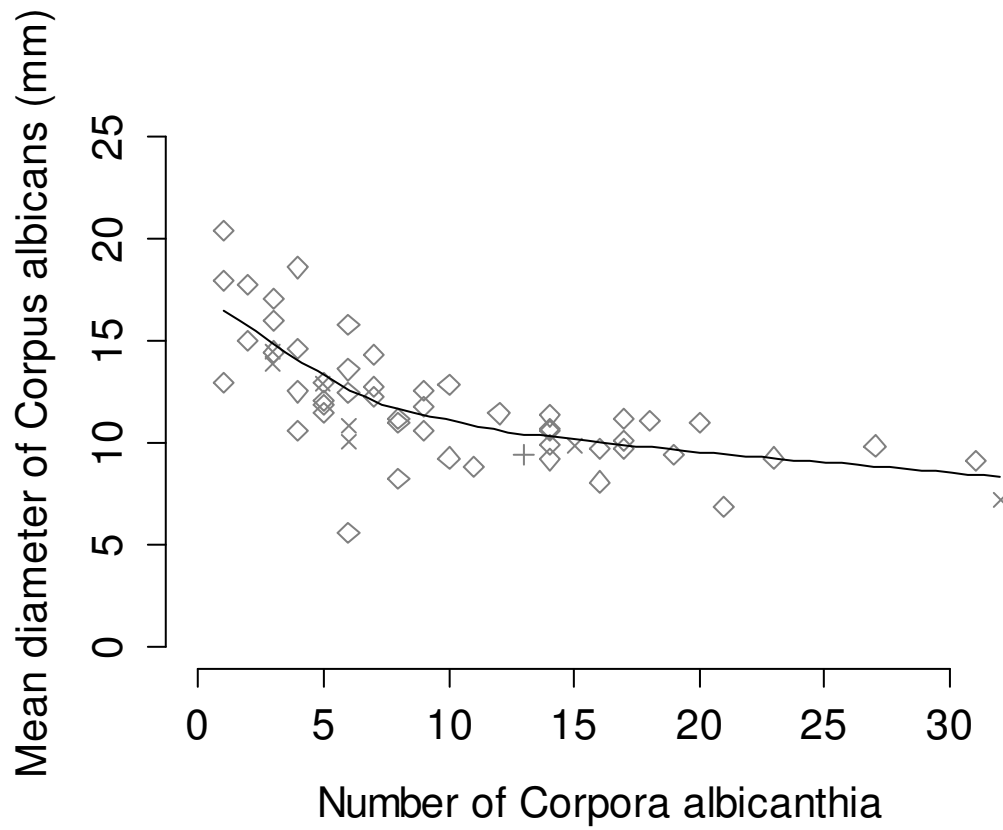
Fig. 9. Standard length with ASP-age in male common minke whales (*Balaenoptera acutorostrata*) from Icelandic waters, caught in the period 2003-2009, (o) immatures, (Δ) pubertal and (+) mature, with von Bertalanffy fitted curve.



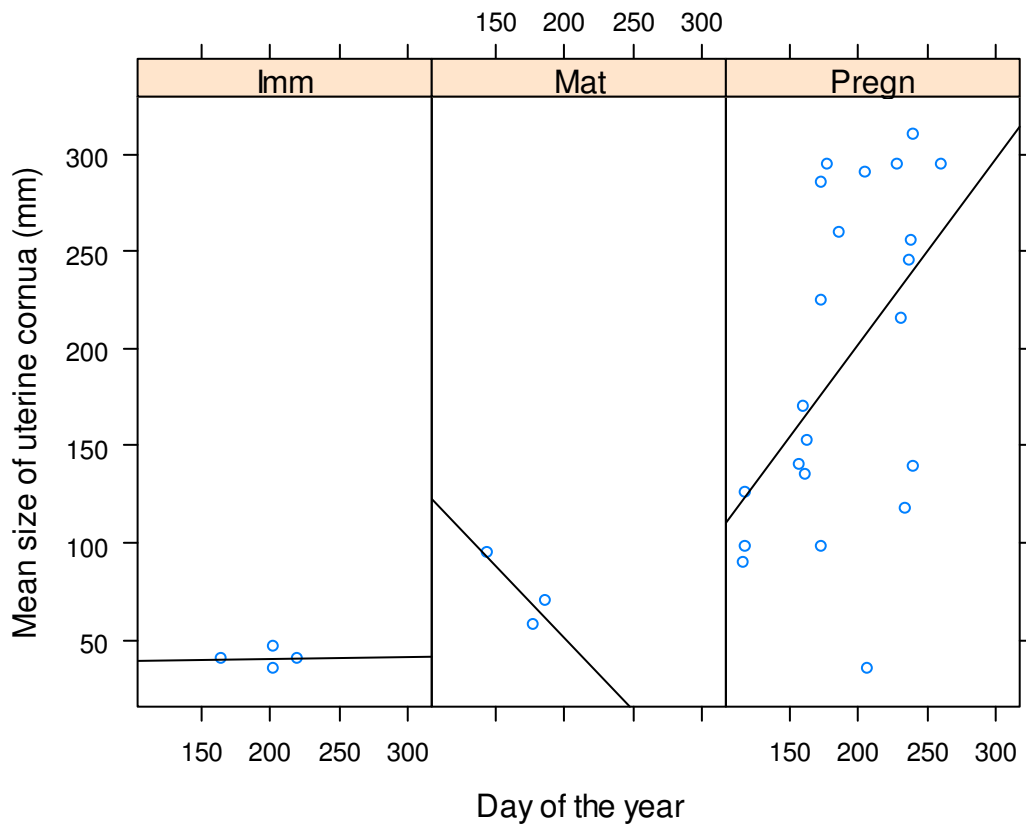
**Fig. 10.** Distribution of total number of corpora (*Corpus luteum*, *Corpora albicantia* and *Corpora abberantia*) in ovaries of female common minke whales (*Balaenoptera acutorostrata*) caught in Icelandic waters in 2003-2009.



**Fig. 11.** Diameter of ovarian bodies, in the ovaries of female common minke whales (*Balaenoptera acutorostrata*), caught in Icelandic waters in 2003-2009, in relation to the maturity stages.



**Fig. 12. Relationship between mean *Corpus albican's* diameter and total number of *Corpora albicantia* in mature females common minke whales (*Balaenoptera acutorostrata*) caught in Icelandic waters, in the period 2003-2009, (+) mature, (x) anoestrous and (◊) pregnant females.**



**Fig. 13. Mean size of uterine cornua in relation to day of the year, in Icelandic common minke whale (*Balaenoptera acutorostrata*) females, showing trends with day in (Imm) immature, (Mat) mature and (Pregn) pregnant females**



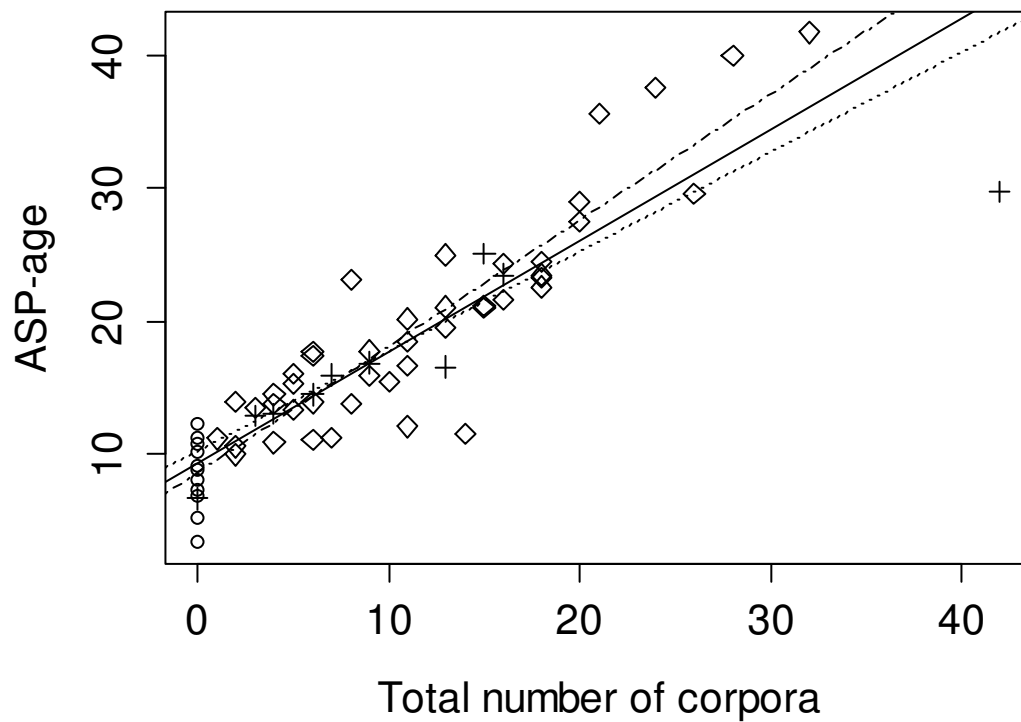
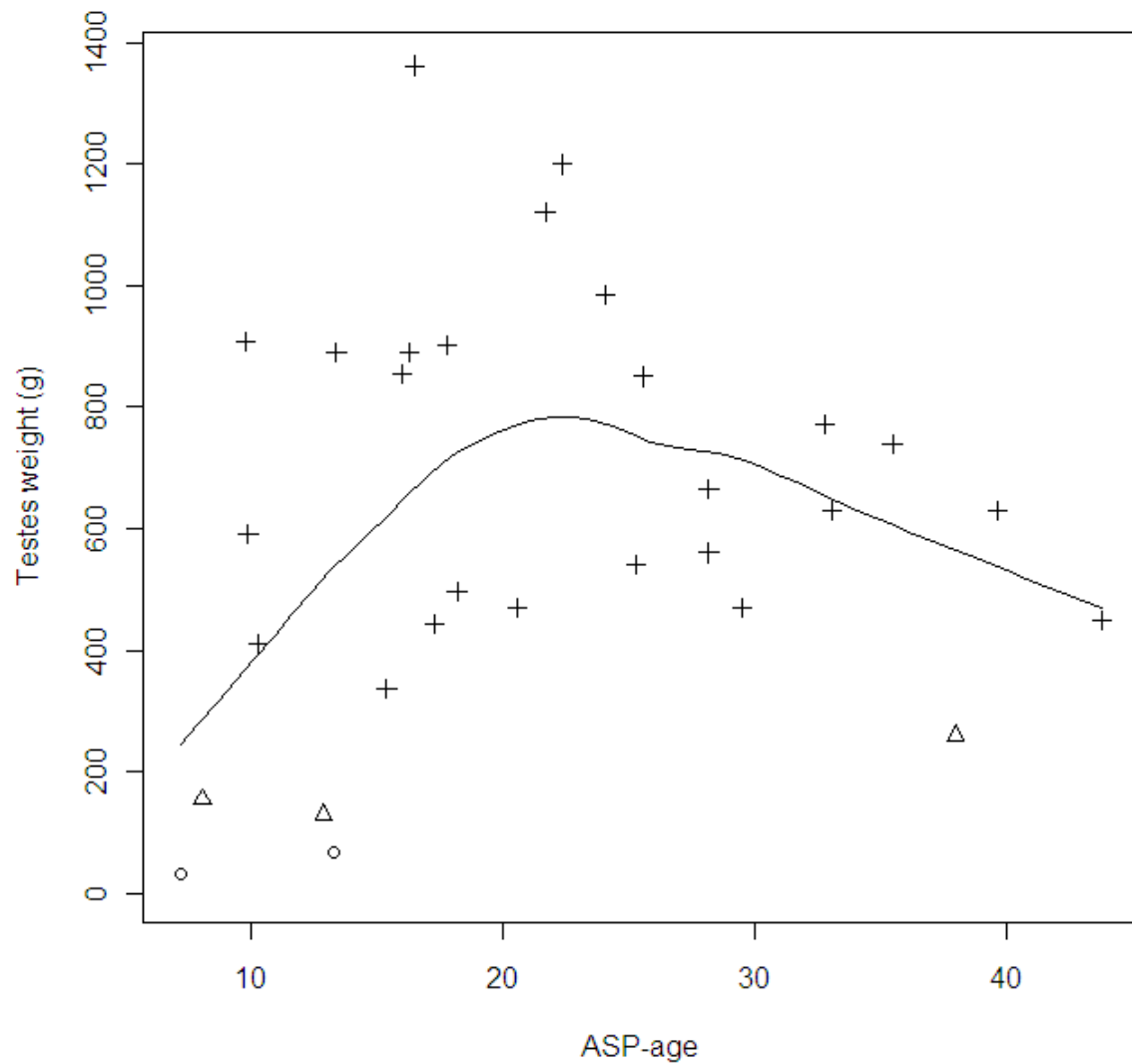
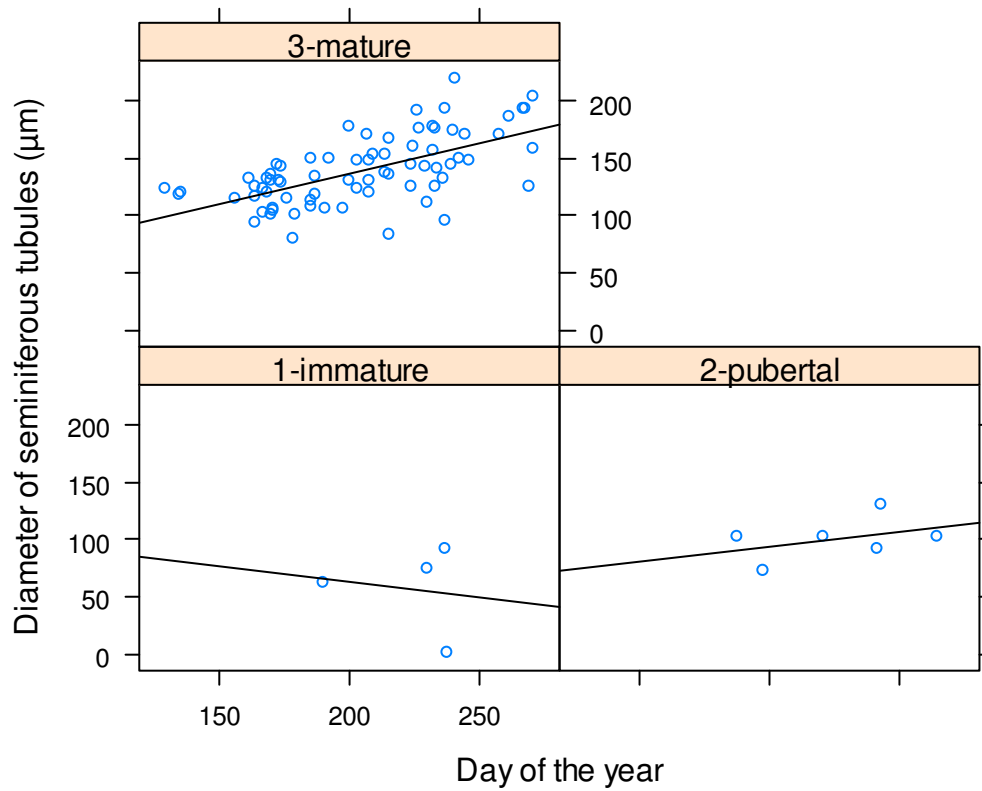


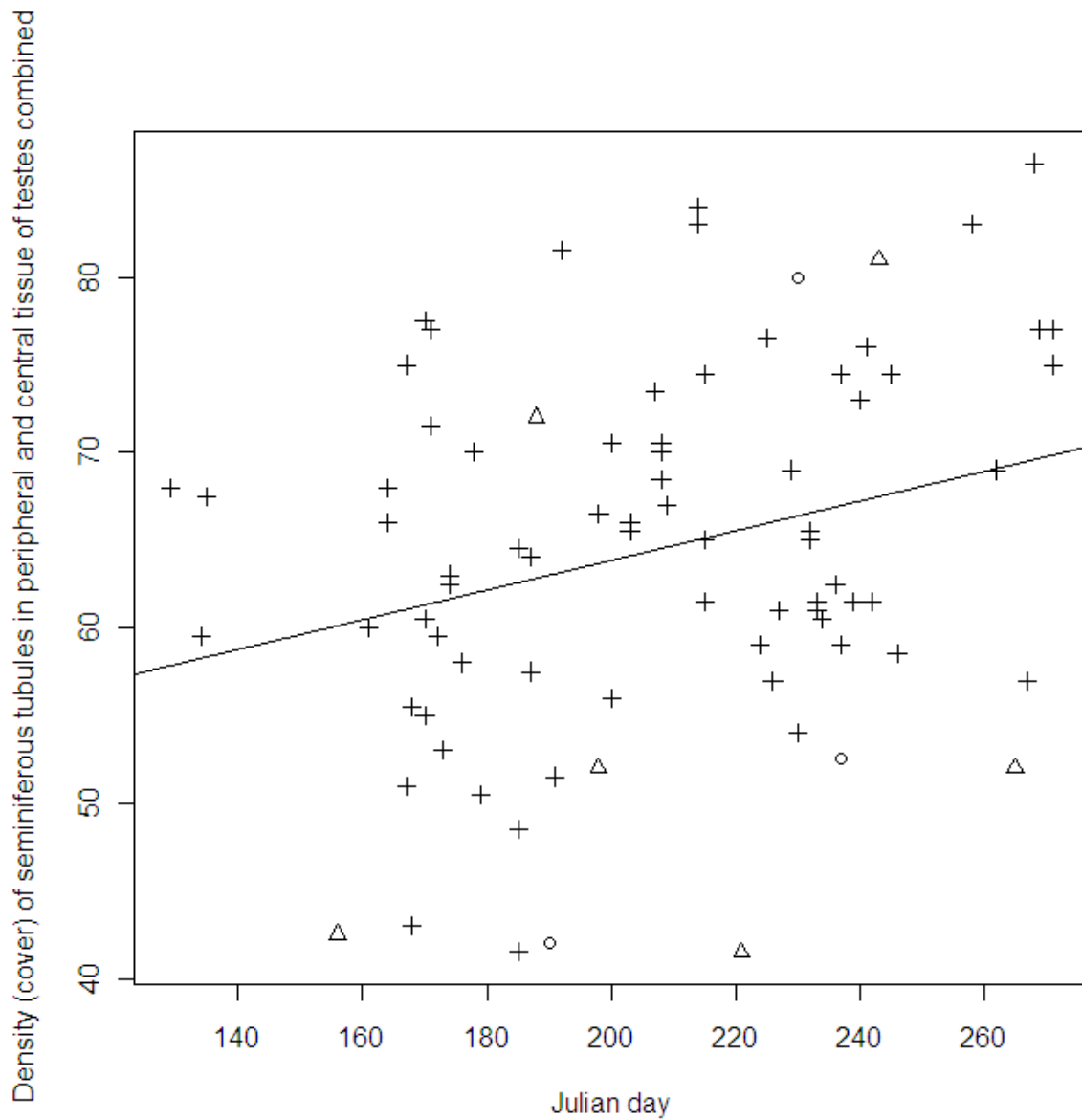
Fig. 14. On the ordinate is ASP-age of common minke whales (*Balaenoptera acutorostrata*) from Icelandic waters, caught in the period 2003-2009, determined with the method of racemisation of aspartic acid (ASP) from the whale eye lens, on the abscissa total number of corpora (*Corpora albicantina*, *Corpora abberantia* and *Corpora lutea*), — ordinary regressions through data points (---) least-trimmed squares regression line and (.....) the resistant regression line, (o) immature, (+) mature and (◊) pregnant animals.



**Fig. 15.** Mean weight of testes in relation to ASP-age, from; (o) immature, (Δ) pubertal and (+) mature common minke whale (*Balaenoptera acutorostrata*) males, caught in Icelandic waters in 2003-2009.



**Fig. 16.** Distribution of measurements of the mean diameter ( $\mu\text{m}$ ) of seminiferous tubules in testes of male common minke whales (*Balaenoptera acutorostrata*) caught in Icelandic waters in 2003-2009, in relation to the day of sampling.



**Fig. 17.** Changes in density (cover) of seminiferous tubules in testes of male common 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.
- Christiansen, F., Rasmussen, M. H., Víkingsson, G. A. & Lusseeau, D. 2012. Minke whales maximize energy storage on their foraging grounds. *ICES Journal of Marine Science?*
- Christensen, I., 1974. Undersøkelser 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.
- Christensen, I., 1992. Age determination of baleen whales. *North Atlantic Studies*, 2, pp.32-35.
- 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.
- DeMaster, D. P., 1978. Calculation of the Average Age of Sexual Maturity in Marine Mammals. *J. Fish. Res. Board Can.* 35: 912-915.
- 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.
- George, J.C. et al., 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* 77:, 77, pp.571-580.
- 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, A., 1962. Population Studies on the minke whale (*B. acutorostrata*) Lacepede. In E. D. le Cren and M. W. Holtgate, eds. *The exploitation 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.

- Kjeld, M., Alfredsson, Á., Ólafsson, Ö., Tryland, M., Christensen, I., Stuen, S., and Árnason, A., 2004. Changes in blood testosterone and progesterone concentrations of the North Atlantic minke whale (*Balaenoptera acutorostrata*) during the feeding season. *Can. J. Aquat. Sci.* 61:230-237.
- 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. and Sigurjónsson, J. 1992. Author's summary of SC/F91/F8: The Icelandic Fin Whale, (*Balaenoptera physalus*): Biological Parameters and Their Trends Over Time. *Rep. Int. Whal. Commn.* 42: 617-618.
- 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., 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. *Rep. Int. Whal. Commn* (special issue), 6, pp.27-50.
- Lockyer, C. & Sigurjónsson, J., 1991. The Icelandic fin whale, (*Balaenoptera physalus*). Biological parameters and their trends over time. Scientific Committee, F91/F8.
- 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.
- Nielsen, N.H. et al., 2012. Application of a novel method for age estimation of a baleen whale and a porpoise. *Marine Mammal Science*.
- Neuenhagen, C., Hartman, M.G., and Greven, H., 2007. Histology and morphometrics of testes of the white-sided dolphin (*Lagenorhynchus acutus*) in bycatch samples from the northeastern Atlantic. *Mammalian Biology* 72(5):283-298.
- 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.
- Olsen, E. et al., 2003. The suitability of mandible growth layers in the common minke whale (*Balaenoptera acutorostrata*) for age determination. *JOURNAL OF CETACEAN RESEARCH AND MANAGEMENT*, 5(2), pp.93-102.
- Olsen, E. & Sunde, J., 2002. Age determination of minke whales (*Balaenoptera acutorostrata*) using the aspartic acid racemization technique. *Sarsia*, 87(1), pp.1-8.

- 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.
- Perrin W.F and Donovan, W.F. (eds) 1984. Report of the Workshop. *Rep. Int. Whal. Commn* (Special Issue 6):1-24.
- Perrin, W. F. and Donovan, G. P. 1984. Reproduction in Whales, Dolphins and Porpoises: Report of the Workshop. *Rep. int. Whal. Comm.* (Special Issue 6):1-24
- 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.
- R Development Core Team 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- 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: skýrsla til stjórnarráðsins. Andvari – *Tímarit Hins íslenska Þjóðvinafélags* 56: 48-110.
- Sæmundsson B. 1937. Fiskirannsóknir 1936-1937: skýrsla til stjórnarráðsins. Andvari – *Tímarit Hins íslenska Þjóðvinafélags* 62: 22-61.
- Sigurjónsson, J. 1995. On the life history and autecology of North Atlantic rorquals. In: Blix A. S., Walløe, L. and Ulltang, Ø. (eds.) *Whales, seals, fish and man*. Elsevier Science B. V. pps: 425-441.
- Sigurjónsson, J. and Víkingsson, G.A., 1997. 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. 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.

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.