# Growth and reproduction in the Icelandic grey seal

### Erlingur Hauksson

Fornistekkur 14, IS-109 Reykjavík, Iceland

# ABSTRACT

Growth and reproduction in grey seals (*Halichoerus grypus* Fabricius, 1791) from Iceland were examined. The oldest Icelandic grey seals obtained were a 36 year old female and a 23 year old male. The longest animals were a 255 cm 13 year old male, and a 230 cm 20 year old female. The heaviest grey seal was an 11 year old male weighing 310 kg. The heaviest female was a 20 year old female that weighed 240 kg. Females reached an asymptotic standard length and weight of 200 (95% CI 196 - 204) cm and 164 (95% CI 157 - 171) kg. Males attained an asymptotic standard length of 243 (95% CI 232 - 254) cm and mass of 279 (95% CI 254 - 306) kg. Investigations of the ovaries and testes indicate that, by the time that females were seven years old, over 90% were pregnant. The average age of sexual maturity of females was 4.0 years (95% CI 3.59 - 4.41) and the average age of first pupping was 5.3 (95% CI 4.95 - 5.72). Average age of sexual maturity for males was 4.9 (95% CI 4.43 - 5.40). Seven out of 8 grey seal males had fully developed testes at the age of 7. All males, 8 years of age and older were mature. Adult (5+ years) females and males are fattest in the summer right before breeding in the autumn, but leanest in the winter after breeding and mating, and in the spring after moulting.

Hauksson, E. 2007. Growth and reproduction in the Icelandic grey seal (*Halichoerus grypus*). *NAMMCO Sci. Publ* 6:153-162.

# INTRODUCTION

The grey seal (*Halichoerus grypus* Fabricius, 1791) is a large phocid, with males attaining over 300 kg in weight. They have a cold temperate to subarctic distribution in the North-Atlantic, with animals from the Northeast Atlantic population occurring as far north as Murmansk, western Russia, and as far west as Iceland (Haug *et al.* 1994, Fig. 1).

In the early 1980's, people in the Icelandic fishing industry were concerned about the possible detrimental effects of a growing unexploited grey seal stock on fisheries, both direct through predation and indirect through their role as the final host of the sealworm (*Pseudoterranova decipiens*) in Icelandic coastal waters (Ólafsdóttir 2001). This concern resulted in more research on the biology of the grey seal in Iceland, (Hauksson 2007, Hauksson and Bogason 1997a,b, Ólafsdóttir and Hauksson 1997, Pálsson 1993).

Early work on grey seals in Iceland led to the species description by Eggert Ólafsson in 1772.

The description *Phoca grypus* in 1791 by Fabricius is likely based on Ólafsson's (Bonner 1981). Thienemann later described it as a species nova, in 1839, but Jónas Hallgrímsson showed that Thieneman was in error and that the Icelandic grey seal was *P. grypus* (Jónsson 1988). Bjarni Sæmundsson (1932) then described the Icelandic grey seal as (*Halichoerus grypus*, Fabricius) in his monograph on Icelandic mammals, and commented on its size, sexual dimorphism and breeding schedule.

The trend in the Icelandic grey seal population has been different from that in other areas. Although there are some small and increasing stocks in the Baltic (Harding *et al.* 2007), on the coasts of Murman (Ziryanov and Mishin 2007), on the coast of Norway (Nilssen and Haug 2007), on the eastern shores of United States of America (Wood *et al.* 2007) and Faroe Islands (Mikkelsen 2007), grey seal stocks around the British Isles and in Canada are quite large and appear to be still increasing (Bowen *et al.* 2003, Duck and



Fig. 1. Typical grey seal breeding habitat: a rocky island off Iceland. (Photo: Erlingur Hauksson)

Thompson 2007, Hammill et al. 2007). However, the Icelandic grey seal stock, is small and decreasing (Hauksson 2007). This makes it interesting to compare its growth and reproductive rates with those of other grey seal populations. Data on asymptotic size are available for British grey seals (Boyd 1984, Bonner 1981, McLaren 1993) and for the north western Atlantic grey seal stock (Murie and Lavigne 1992, McLaren 1993, Mohn and Bowen 1996, Hammill and Stenson 2000, Lesage and Hammill 2001). Reproduction data for grey seals is also available, from Norwegian waters (Wiig 1991), the Northwest Atlantic (Mansfield 1978, Hammill and Gosselin 1995), and from the British Isles and Faroe Islands (Bonner 1981, Boyd 1985). This paper examines recent information on growth and maturity of grey seals in Icelandic waters.

# MATERIALS AND METHODS

Whole animals or samples including the lower jaw, stomach and sex-organs were obtained from local fishers, special collectors and seal-hunters (Table 1). Date of collection was known within  $\pm 15$  days. Samples were preserved frozen. Age in years was determined by counting growth-layers in the cementum of a thin-transverse-section (0.4-0.6 mm) of the canine tooth, cut with a low

speed saw near the base of the tooth. The best position of the transverse cut was determined by longitudinal sectioning of several teeth (Mansfield and Fisher 1960). A binocular-dissecting microscope with 6X to 50X magnification and transmitted light was used (Bowen *et al.* 1983).

Ventral curve linear standard length (American Society of Mammalogists 1967, McLaren 1993) of animals was measured to the nearest cm from the nose to the end of the tail, with the animals lying on their backs. Blubber thickness was measured to the nearest cm, by making a ventral cut through the skin and fat at the lower end of the sternum. Body mass was determined with a Salter scale (for 0 - 999 kg loads) to the nearest kg, but was not corrected for blood loss. Changes in size at age were described using a von Bertalanffy growth model  $A_x = A \infty_x (1 - exp(-a(x - x_0)))b$  (McLaren 1993), where  $A_x$  and  $A\infty$  are either length (L) or mass (M) at age x in years and asymptotic length or mass in cm or kg respectively. The variable  $x_0$  was set at -0.59, and was used to fit standard length or mass in relation to age, as recommended by McLaren (1993). The coefficient, a, determines the rate of approach to the asymptote and b determines the curvlinearity of this approach (Fig. 2. and 3.).  $X_0$  is negative when birth is taken at age 0. Standard length was measured on all foetuses

Table 1. Grey seals ( <i>Halichoerus grypus</i> ) females and males, foetus and 0+ animals, collected in the period 1980-1993, number in each age group, and foetuses after months, measured and/or weighed animals in parentheses. n.d not determined. *One foetus of unknown sex included.	seals ( <i>f</i> 1 age g etus of	<i>Halichc</i> Iroup, å unkno	<i>perus g</i> and foe wn sey	<i>rypus</i> ) fe tuses aft < include	males and er months d.	d males, , measu	foetus ar ired and/c	nd 0+ ani or weigh€	imals, col ed animal	llected in t Is in paren	the period	1980-19 .d not (	93, leter-
Months	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Νον	Dec	Total
Females													
Foetus				3 (3)*	16 (16)	3 (3)*	10 (10)	7 (7)					39 (39)
Pups	2 (2)	6 (0)	3 (0)	7 (0)	65 (1)	3 (0)	10 (0)		4 (4)	136 (136)	58 (58)	1 (1)	295 (202)
1 yr					11 (0)		6 (0)	2 (1)					19 (1)
2 yr					6 (0)	2 (1)	(0) 6	2 (1)	1 (0)				20 (2)
3 yr				1 (0)	8 (1)	1 (0)	6 (0)	3 (1)	2 (1)	4 (0)	1 (0)		26 (3)
4 yr		1(1)			5 (0)	1 (0)	2 (0)	2 (0)		7 (7)	4 (4)		22 (12)
5+ yrs	1 (1)	1 (0)	2 (1)	7 (1)	42 (6)	14 (1)	59 (7)	38 (3)	23 (12)		262 (53)	76 (30)	525 (115)
Age n.d.									1 (1)	20 (20)	3 (3)		24 (24)
Total 0+ females	3 (3)	8 (1)	5 (1)	15 (1)	137 (8)	21 (2)	92 (7)	47 (6)	31 (18)	429 (216)	142 (95)	1 (1)	931 (359)
Males													
Foetus				2 (1)	20 (20)	6 (6)	20 (20)	7 (7)					55 (54)
Pups	2(0)		5 (0)	11 (0)	64 (2)	6 (0)	4 (0)	1 (1)	6 (6)	168 (168)	62 (61)	1 (0)	330 (238)
1 yr				3 (0)	7 (0)	1 (0)	5 (0)	1 (0)		1 (0)	2(0)		20 (0)
2 yr		1 (0)	2 (1)	2 (0)	6 (0)	1 (0)	5 (1)	3 (0)	1 (0)				21 (2)
3 yr	1 (1)			1 (0)	6 (1)		3 (1)	2 (0)	1 (1)		1 (0)		15 (4)
4 yr	1 (0)	1 (1)	2 (2)		6 (2)		4 (1)	2 (0)	1 (1)		1 (0)		18 (7)
5+ yrs	3 (2)	3 (3)	2 (1)	8 (6)	11 (1)	6 (6)	19 (8)	20 (5)	29 (3)	107 (20)	20 (8)		228 (63)
Age n.d.								1 (1)		6 (6)	4 (4)		11 (11)
Total 0+ males	7(3)	5 (4)	11 (4)	25 (6)	100 (6)	14 (6)	40 (11)	30 (7)	38 (11)	282 (194)	90 (73)	1 (0)	643 (325)

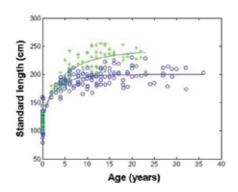


Fig. 2. Growth in standard length with age of female (o) and male (+) Icelandic grey seals (Halichoerus grypus) described with the von Bertalanffy model (see McLaren 1993).

recovered and foetuses were weighed to the nearest 5 grams. Foetal growth in length was examined by fitting the data to a Gompertz growth equation. The mean date of birth was set on 15 October, day 289 (see Yunker *et al.* 2005).

Ovaries and testes were preserved frozen. Transverse, systematic cuts were made into the ovaries, and the sections were examined macroscopically for evidence of follicular activity, presence of corpus luteum, or corpora albicans. Females were considered mature if evidence of follicular growth was found, and when the largest diameter of a follicle exceeded 5 mm (Boyd 1983). Females were also classified as nulliparous (female has never been impregnated), primiparous (pregnant only once, regardless of whether the pregnancy is carried to term) and multiparous (previously pregnant more than once and either pregnant or non pregnant at the time of collection). Testes (with epididymis), which had been kept frozen, were weighed with 5 g accuracy and males with a testes average weight >75grams considered mature, with reference to the fitted Gompertz curve of testes mass to age (Fig. 4). The average age of sexual maturity (presence or absence of corpus luteum) and average age of first pregnancy (presence or absence of foetus) of females and average age of sexual maturity of males (testes mass > 75 grams) were estimated using the algorithm developed for marine mammal populations by DeMaster (1978).

Statistical analyses were performed with Mathlab® 7.1 Statistical Toolbox version 5.1. The routines 'normplot' and 'dfittool' were used to test for normality of data. Non linear least square regression of standard length and weight on age and estimation of the power curve of weight on length were done with the 'nlinfit' routine, and the measured fat thickness, which had close to normal distribution (log likelihood -1177.87), was investigated for significant differences with analysis of variance with sex, collection month and their interaction as factors, with the 'anovan' routine. Stepwise multiple regression was performed with the 'stepwise' and 'regress' routines.

### RESULTS

### Age distribution, length and weight of collected animals

A total of 37 females, 55 males and 2 foetuses of unknown sex were collected during the months April to August. The females obtained in September were all from breeding sites and had already given birth (Table 1). The smallest foetus examined was collected in April 1993. The sex of this foetus is not known. It had a standard length of 5.5 cm and weighed 10 grams. The smallest foetuses of known sex were 16 cm and 105 grams and 15 cm and 135 grams for females and males respectively, collected in May 1990 and in April 1993 respectively. The largest female foetus found in uteri, had a standard

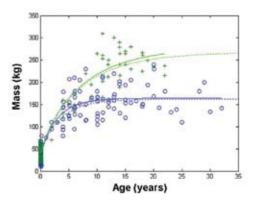


Fig. 3. Change in mass at age of female (o) and male (+) Icelandic grey seals (Halichoerus grypus) described with the von Bertalanffy model for growth (solid lines). Calculated mass at age, by using estimated standard length at age and the power function of weight on length (dotted lines), is presented for comparison.

Table 2. P parenthes		values for	von Berta	alanffy gr	owth mode	el with 959	% confide	nce interv	als in
	A∞			а			b		
LENGTH									
Males	242.9	(232.0,	253.8)	0.124	(0.072,	0.176)	0.283	(0.249,	0.317)
Females	200.1	(196.2,	203.9)	0.252	(0.169,	0.334)	0.286	(0.241,	0.331)
MASS									
Males	279.2	(254.5,	305.9)	0.116	(0.072,	0.159)	0.716	(0.642,	0.790)
Females	164.1	(156.9,	171.3)	0.332	(0.215,	0.428)	0.849	(0.699,	0.999)

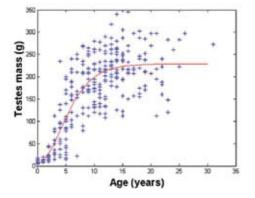


Fig. 4. Mean mass of male grey seal (Halichoerus grypus) testes in relation to age, according to the Gompertz growth model.

length of 78 cm and weighed 10.3 kg. The largest male foetus had a standard length of 79 cm and weighed 12.8 kg male. Both foetuses were obtained from female grey seals in August 1992. The smallest newborn pups found on breeding sites were a 88 cm and 10 kg female and a 83 cm and 12 kg male, collected in November 1990 and October 1992 respectively. The biggest nursing pups observed were a 136 cm long, 68 kg female and a 141 cm long, 71 kg male. A total of 931 females and 643 males 0+ of age were sampled (Table 1). The oldest animals sampled were a 36 year old female and a 23 year old male. The longest animals were a 255 cm, 13 year old male, and a 230 cm, 20 year old female. The heaviest grey seal was a 310 kg, 11 year old male. The heaviest female was a 20 year old animal weighing 240 kg.

#### Length and weight relationships

The relation of weight (W<sub>f</sub>) to length (L<sub>f</sub>) followed a power curve for foetuses and 0+ grey seals. The relationship for foetuses was;  $W_f = 0.0001096L_f^{2.621}$ ; (adjusted  $R^2 = 0.97$ , df = 90, RMSE (Root

Mean Squared Error) = 0.6239; 95% CI for intercept 0.00004157 - 0.0001776 and for the exponent 2.476 - 2.767)

Table 3. Total numband percentage sho				0 1	`		•	•••	) collect	ted (N),	number
Age	0	1	2	3	4	5	6	7	8	9	10+
N	96	17	20	26	18	38	41	28	25	27	366
CL	0	0	2	8	11	29	34	27	22*	24**	339***
Foetus	0	0	1	7	6	29	34	27	23	26	345
% females with CL	0.0	0.0	10.0	30.8	61.1	76.3	82.9	96.4	91.7	92.3	94.2
% females with foetus	0.0	0.0	5.0	26.9	33.3	76.3	82.9	96.4	92.0	96.3	94.3

\* Ovaries missing in one sample, but foetus present.

\*\* Ovaries missing in two samples, but foetus present.

\*\*\* Ovaries missing in six samples, but foetus present.

and for 0+ animals;  $W_{0+} = 0.0001933L_{0+}^{2.575}$ ; (adjusted  $R^2 = 0.93$ , df = 465, RMSE = 17.44386; 95% CI for intercept 0.0001203-0.0002662 and for the exponent 2.504- 2.646). A better fit was obtained by incorporating girth and blubber thickness data into the equation for 0+ animals resulting in the relationship:

$$\begin{split} &\log_{e}M = -8.8275 + 2.0173\log_{e}L + 0.6829\log_{e}G \\ &+ 0.0485F, (R^2 = 0.96, F_{3,238} = 3212.03, P < 0.001), where L is length (cm), G is a half-girth measurement over the back of the seals dorsally right behind the fore-flippers from axilla to axilla (cm) and F is the sternum blubber thickness (cm). \end{split}$$

### Growth in length and weight

The increase in foetus length was described by a Gompertz growth function, in relation to date. On day 289 (15 October), the mean birthing date, the estimated standard length of a foetus was 90.0 cm. The weight at birth, estimated from the mass-length equation above was 14.5 kg. Two newborn pups examined at the breeding sites had a body mass of 11 kg for the female and 10 kg for the male. For 0+ animals, growth at age was described by fitting a Von Bertalanffy growth curve to the length (Lx) and weight (Wx) data (Table 2). Males were about 40 cm longer and 115 kg heavier than females (Fig. 2, 3). Differences in patterns of growth were observed between males and females. Females grew rapidly from ages 1 to 5 years, then growth began to slow, reaching an asymptote by the age of 9 years. For males, growth was rapid between the ages of 1 and 9 years old, then slowed reaching an asymptote by the age of 15 years.

### Reproduction

Corpora lutea were first observed in 2 females as young as 2 years old (n = 20) (Table 3). A foetus was detected in one two year old female, indicating an age at first birth if carried successfully to term of 3 years old. The proportion of females with corpora lutea was much higher than the proportion of females with a foetus present among females aged 2 to 4 years old. This difference was not noticeable among females aged 5 years and older. By the time that animals were 7 years old, over 90% of females

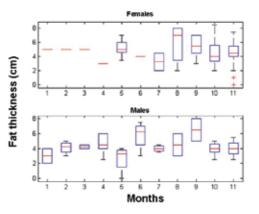


Fig. 5. Seasonal changes, by month, in condition as indicated by fat-thickness at lower end of sternum of adult (5+ years) female and male grey seals (Halichoerus grypus).

were pregnant (Table 3). The average age of sexual maturity of females was 4.0 years (95% CI 3.59 - 4.41) and average age of first pregnancy was 5.3 (95% CI 4.95 - 5.72). Over 95% of females older than 9 years were mature. At age 5, the great majority, 82.9% (95% CI 70.4 - 95.3%) of females were multiparous.

The Gompertz growth curve gave a reasonably good fit to the testes-mass to age data, but the variability around the best line was great (Fig. 4). The average age of sexual maturity for males was 4.9 (95% CI 4.43 - 5.40). Seven out of 8 of grey seal males had fully developed testes at the age of 7. All males 8 years of age and older were mature.

### Seasonal changes in condition

There was a significant interaction between sex and age-groups (P = 0.02), so fat-thickness in the 2 sexes was analysed separately. Males had thicker fat at the lower end of sternum than females. For both sexes the interaction between month of collection and age-group was highly significant (P < 0.001). The relation between fat-thickness and month was different for the 3 age-groups. Pups and seals1 - 4 years of age were not analysed further, because the pups were obtained in the autumn and too few animals between the ages of 1 and 4 were sampled (Table 1, numbers in parentheses). On average, females 5+ years old were thinner in the winter and spring after breeding and moulting than in July to September. Males 5+ years of age were also leanest during the early spring and in the winter after the mating time. This was however not a very strong pattern, and animals with little fat could be found all year round, with their condition in the autumn being highly variable (Fig. 5).

# DISCUSSION

The average weight of a full-term foetus, extrapolated from these data, was about 15 kg for the Icelandic grey seal. This is similar to observations from British grey seals, where the weights at birth are 15 and 16 kg for females and males respectively (Bonner 1981).

Icelandic grey seals reached asymptotic lengths of about 243 and 200 cm for males and females respectively. This was similar to asymptotic lengths of 230 and 201 cm for males and females respectively from the Northwest Atlantic (McLaren 1993), but larger than asymptotic lengths of 207 and 180 cm for British grey seals (Bonner 1981). The asymptotic weight of males is about 115 kg heavier than the females. However, this is likely an overestimation of the degree of dimorphism between the sexes because much of the mass data was collected during the breeding season. Although both males and females lose mass at this time of year, females lose mass at a much more rapid rate than males as a result of energy transfer to the pups during lactation (Baker et al. 1995, Tinker et al. 1995).

Among grey seals from Iceland, the average age of sexual maturity determined from the presence of a corpus luteum using the method of DeMaster (1978) was 4.0 years (95% CI 3.59 - 4.41). The average age of first pregnancy, determined by the presence of a foetus was slightly greater at 4.3 years (95%CI 3.95-4.72). These are similar to estimates from the British Isles and the Faroe Islands (Bonner 1981, Boyd 1985). Estimates of age at sexual maturity are also available from Norwegian and Northwest Atlantic waters, but these are expressed as the age at which animals would give birth (Wiig 1991, Hammill and Gosselin 1995). When one year is subtracted to make these comparable to the current dataset, then age at sexual maturity for Icelandic grey seals is similar to estimates from these areas.

The reproductive cycle of grey seals males is probably such that sperm production is at its maximum during mating during September to November, but quiescent during other parts of the year (Gardiner et al. 1999). Among males, testis mass increases rapidly between the ages of 4 to 10 years. Most males were sexually mature by the age of 8 years, with an average age of sexual maturity of 4.9 years. This is approximately one year earlier than has been observed in the Northwest Atlantic (Hammill and Gosselin 1995). Although virtually all males may be sexually mature by 8+ years, these animals appear to be limited to the periphery of the breeding colony (Hewer 1964), occasionally succeeding in copulating with females as transient males (Godsell 1991). On Sable Island, in the Northwest Atlantic, few animals are capable of maintaining tenure among whelping females before the age of 11 to 12 years (Boness and James 1979, Godsell 1991).

The Icelandic grey seal population is quite small, with current estimates suggesting a declining population of 4,100 - 5,900 animals (Hauksson 2007). Unlike other populations, the Icelandic population is subject to small-scale hunting operations to limit perceived impacts on commercial fisheries. Current estimates are much lower than historical perceptions of the population and suggest that the current population is much below environmental carrying capacity. The larger size of the Icelandic grey seal compared to its nearest neighbors in the United Kingdom, early age at sexual maturity and high reproductive rates are similar to what has been reported for the much larger increasing Northwest Atlantic population of grey seals (McLaren 1993, Hammill and Gosselin 1995, Mohn and Bowen 1996, Bowen et al. 2003, Duck and Thompson 2007), which would suggest that density dependent factors in response to low abundance are operating in this population.

### ACKNOWLEDGEMENTS

Biologists Droplaug Ólafsdóttir, Guðbjörn Karlsson and Valur Bogason, and Veterinarian Lars Hansen assisted in processing of the seal samples. In 1992-93, this research was a part of the Multispecies Research Program of the Marine Research Institute in Reykjavík, and sponsored by the Icelandic Fishery Ministry (Pálsson 1993). Icelandic fish-industry and fisheries' organisations also funded this research, which is highly appreciated. Two anonymous reviewers, and 2 of the volume's editors, Droplaug Ólafsdóttir and Dr. M.O. Hammill, provided valuable comments on the manuscript and suggestions for improvements.

### REFERENCES

- American Society of Mammologists. 1967. Standard measurements of seals. J. Mammal. 48:459-462.
- Baker, S.R., Barrette, C. and Hammill, M.O. 1995. Mass transfer during lactation of an ice-breeding piniped, the grey seal (*Halichoerus grypus*), in Nova Scotia, Canada. J. Zool., London 236:531-542.
- Bonner, W.N. 1981. In: Ridgway, S.H. and Harrison, R.J. (eds.); *Handbook of Marine Mammals 2. Seals*. Academic Press, London, 111-144.
- Boness, D.J. and James, H. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. J. Zool., London 188:477-500.
- Bowen, W.D., Sergeant, D.E. and Øritsland, T. 1983. Validation of age estimation in the harp seal, *Phoca groenlandica*, using dentinal annuli. *Can. J. Fish. Aquat. Sci.* 40:1430-1441.
- Bowen, W.D., McMillan, J. and Mohn, R. 2003. Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. *ICES J. Mar. Sci.* 60:1265-1274.
- Boyd, I.L. 1983. Luteal regression, follicle growth and the concentration of some plasma steriods during lactation in grey seals (*Halichoerus grypus*). J. Reprod. Fertil. 69:157-164.
- Boyd, I.L. 1984. The relationship between body condition and the timing of implantation in pregnant grey seals (*Halichoerus grypus*). J. Zool., London 203:113-123.
- Boyd, I.L. 1985. Pregnancy and ovulation rates in Grey seals (*Halichoerus grypus*) on the British coast. J. Zool., London. 205:265-272.
- DeMaster, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Bd. Can. 35:912-915.
- Duck, C.D. and Thompson, D. 2007. The status of grey seals in Britain. *Nammco Sci. Publ.* 6:69-78.
- Gardiner, K.J., Boyd, I.L., Follett, B.K., Racey, P.A. and Reijnders, P.J.H. 1999. Changes in pituitary, ovarian, and testicular activity in harbour seals (*Phoca vitulina*) in relation to season and sexual maturity. *Can. J. Zool.* 77:211-221.
- Godsell, J. 1991. The relative influence of age and weight on the reproductive behaviour of male grey seals *Halichoerus grypus*. J. Zool., London 224:537-551.

- Hammill, M.O. and Gosselin, J.F. 1995. Grey seal (*Halichoerus grypus*) from the Northwest Atlantic: female reproductive rates, age at first birth, and age of maturity in males. *Can. J. Fish. Aquat. Sci.* 52:2757-2761.
- Hammill, M.O. and Stenson, G.B. 2000. Estimated prey consumption by harp seals (*Phoca groen-landica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. J. Northw. Atl. Fish. Sci. 26:1-23.
- Hammill, M.O., Gosselin, J.F. and Stenson, G.B. 2007. Abundance of Northwest Atlantic grey seals in Canadian waters. *NAMMCO Sci. Publ.* 6:99-115.
- Harding, K.C., Härkönen, T., Helander, B. and Karlsson, O. 2007. Population assessment and ecological risk analysis of the Baltic grey seal (*Halichoerus grypus*). NAMMCO Sci. Publ. 6:33-56.
- Haug, T., Henriksen, G., Kondakov, A., Mishin, V., Nilssen, K.T. and Røv, N. 1994. The status of grey seals *Halichoerus grypus* in North Norway and on the Murman coast, Russia. *Biol. Conserv.* 70:59-67.
- Hauksson, E. 2007. Abundance of grey seals in Icelandic waters, based on trends of pup-counts from aerial surveys. *NAMMCO Sci. Publ* 6:85-97.
- Hauksson, E. and Bogason, V. 1997a. *Stofnþættir landsels og útsels* (Biology of common and grey seal). Hafrannsóknastofnunin, fjölrit 53:297-317. (In Icelandic).
- Hauksson, E. and Bogason, V. 1997b. Comparative feeding of grey (*Halichoerus grypus*) and common seals (*Phoca vitulina*) in coastal waters of Iceland, with a note on the diet of hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*). J. Northw. Atl. Fish. Sci. 22:125-135.
- Hewer, H.R. 1964. The determination of age, sexual maturity, longevity and a lifetable in grey seal (*Halichoerus grypus*). *Proc. Zool. Soc.* 142(4):593-624.
- Jónsson, J. 1988. *Hafrannsóknir við Ísland I. Frá öndverðu til 1937* (Oceanographic research in Iceland, before the year 1937). Bókaútgáfa Menningarsjóðs, Reykjavík, 340 pp. (In Icelandic).
- Lesage, V. and Hammill, M.O. 2001. The status of the grey seal, *Halichoerus grypus*, in the Northwest Atlantic. *Can. Field Nat.* 115:653-662.
- Mansfield, A.W. 1978. Reproduction of the grey seal *Halichoerus grypus* in eastern Canada. ICES Doc. C.M. 1978/N:13.
- Mansfield, A.W. and Fisher, H.D. 1960. Age Determination in the Harbour Seal, *Phoca vitulina* L. *Nature* 186:92-93.
- McLaren, I.A. 1993. Growth in pinnipeds. Biol. Rev. 68:1-79.
- Mikkelsen, B. 2007. Present knowledge of grey seals (*Halichoerus grypus*) in Faroese waters. *NAMMCO Sci. Publ.* 6:79-84.
- Mohn, R. and Bowen, W.D. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Can. J. Fish. Aquat. Sci.* 53:2722-2738.
- Murie, D.J. and Lavigne, D.M. 1992. Growth and feeding habits of grey seals (*Halichoerus grypus*) in northwestern Gulf of St. Lawrence, Canada. *Can. J. Zool.* 70:1604-1613.

- Nilssen, K.T. and Haug, T. 2007. Status of grey seals (*Halichoerus grypus*) in Norway. *NAMMCO Sci. Publ.* 6:23-31.
- Ólafsdóttir, D. 2001. Review of the ecology of sealworm, *Pseudoterranova* sp(p). (Nematoda: Ascaridoidea) in Icelandic waters. *NAMMCO Sci. Publ.* 3:95-112.
- Ólafsdóttir, D. and Hauksson, E. 1997. Anisakid (Nematoda) infestations in Icelandic grey seals (*Halichoerus grypus* Fabr.). J. Northw. Atl. Fish. Sci. 22:259-269.
- Pálsson, Ó.K. 1993. Icelandic multi species project. In: Proceedings of a workshop on predation processes and predation models. Nordic seminar in Stykkishólmur, 7.-11. September, p. 68-78. Copenhagen: Nordic Council of Ministers.
- Sæmundsson, B. 1932. *Íslensk dýr II. Spendýr* (Icelandic mammals). Reykjavík. Bókaverslun Sigfúsar Eymundssonar, 437 pp. In Icelandic.
- Tinker, M.T., Kovacs, K.M. and Hammill, M.O. 1995. The reproductive behavior and energetics of male grey seals (*Halichoerus grypus*) breeding on a land-fast ice substrate. *Behav. Ecol. Sociobiol.* 36:159-170.
- Wiig, Ø. 1991. Demographic parameters for Norwegian Grey seals (*Halichoreus grypus*). Fauna norvegica, Series A 12:25-28.
- Wood, S.A., Brault, S. and Gilbert, J.R. 2007. Aerial Surveys of Grey Seals in the Northeastern United States. NAMMCO Sci. Publ. 6:117-121.
- 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.
- Ziryanov, S.V. and Mishin, V.L. 2007. Grey seals on the Murman coast, Russia: status and present knowledge. *NAMMCO Sci. Publ.* 6:13-21.