Abundance of grey seals in Icelandic waters, based on trends of pup-counts from aerial surveys

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ABSTRACT

Grey seals (*Halichoerus grypus* Fabricius, 1791) are distributed all around the Icelandic coast. The majority of the population breeds on the west- and northwest shores, with a second high density in the breeding distribution on the southeast coast of Iceland. During the last 5 decades the Icelandic grey seals have dispersed from the west- to the northwest-, the north- and the northeast-coast. The breeding period occurs from the middle of September to early November, with a maximum in mid October. The time of peak pupping shows some variation, beginning earlier along the west coast and later in the north and southeast. Seven aerial surveys to estimate pup production in Iceland were flown during October to November during the period from 1980 to 2004. Pup counts of the Icelandic grey seal, at all breeding sites combined, have been decreasing annually by about 3% (±1% s.e.), during the period 1982-2002. During the period 1990-2002, this downward trend doubled to about 6% annually. The abundance of the grey seal around Iceland in the year 2002 was estimated to be 4,100 to 5,900 animals. This is higher than estimates of around 2,000 animals during the 1960s, but much less than the estimated population of 8,000 to 11,500 in 1982.

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INTRODUCTION

Grey seals (*Halichoerus grypus* Fabricius, 1791) occur throughout the year around Iceland (Fig. 1). In the past, they were hunted for food and skins on the beaches during breeding and moulting, with a special wooden seal-bat (140 cm long, 4 cm in diameter at the handle to 8 cm at the heavier end, with or without iron spikes). This hunting activity often involved the co-operation of many hunters from several farms for the benefit of people in the whole county. The earliest anecdotal evidence for grey seal hunting is from the 1330's, from the southeast coast of Iceland. There is some evidence for large historical catches: for example, in 1750, 10 hunters clubbed 51 adults and 150 pups in 3 hours, on Öræfi in southeast Iceland. On 21 October, 1785, a hunter assisted by 2 young boys clubbed 70 adults and 120 pups, also on Öræfi. On the island of Vigur the autumn catch was often 70 - 90 pups and about 20 pups in Hrollaugseyjar, located off the southeast coast. On the western shores, old catch statistics are also available. There, 150 pups were regularly clubbed on the island and skerries belonging to the farm Fjörður on the northern shores of Breidafiord, West Iceland. Some islands in Breidafiord are named because harvesting occurred there, e.g. "Drápssker" (Killing-skerries) (Kristjánsson 1980). In recent years, the skins from grey seals have had little value and are rarely sold. In 1962, the Marine Research Institute began collecting catch data. Beginning in 1982 fisheries and fish-industry organisations started promoting seal-hunting (MRI 2005). Harvested grey seals have been used in food mixtures for fur-bearing animals and human consumption. The skin has been used domestically as leather and for garments.

Fig. 1. *Grey seals on a beach in Iceland. (Photo: Erlingur Hauksson)*

Grey seals are distributed all around the Icelandic coast (Fig. 2). They appear to form a discrete group, and based on the low rate of tag returns there is little evidence of exchange with the large colonies found in the United Kingdom (Bonner 1972, Hauksson 2007). There have not been any recoveries since the Bonner study. The grey seals occupy more remote areas than the harbour seal (*Phoca vitulina*) when breeding and moulting. Over the last few decades there has been a movement of people away from the coastal farms towards the towns and cities and there is evidence for grey seals occupying rocks and islands in areas where farms have been abandoned (Hauksson unpublished data).

The shooting of grey seals as well as other seals is generally allowed in Icelandic waters, but prohibited by law in Breidafiord, West Iceland. There, only traditional sealing methods are allowed, such as clubbing and catching in nets. Grey seals along with all animals and the soil are protected on the island of Surtsey (Hauksson 1992).

Throughout much of the year, large numbers of grey seals were traditionally found off the west, northwest and the southeast coasts of Iceland. Over the last 5 decades, the range of grey seals has expanded and animals now occur along the west and north coasts of Iceland as far east as Melrakkaslétta (Fig. 2). However, beginning in 1990, there was an increase in hunting, leading to a reduction in the distribution of animals along the coast, with the disappearance of animals from the northeast coast at Skinnalónsey on Melrakkaslétta.

Breeding occurs during October-November. Breeding colonies are limited to the southeast and northwest coasts. During moulting, the seals are seen in large groups in remote areas, often the same areas as they breed, but not in every case. Marked young animals have been found to travel long distances between coastal areas, and tagging has shown some exchange between breeding colonies (Einarsson 1993).

Grey seals are top predators in Icelandic waters and may compete with cormorants (*Phalacrocorax carbo*) on the west coast of Iceland during autumn, where both species feed heavily on short-spined sea scorpions (*Myoxocephalus scorpius*) (Lilliendahl *et al.* 2004). Evidence for such competition between seals and cormorants has also been observed in the North Sea (Härkönen and Heide-Jørgensen 1991). The

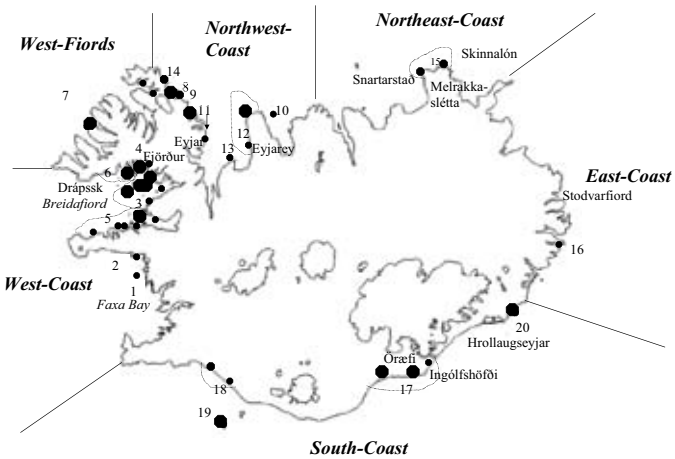

Fig. 2. *Distribution of grey seals in Icelandic waters. Division of the coast into areas and main rookeries: Hvalseyjar (1), Tjaldurseyjar (2), Frameyjar (3), Skálmarnes (4), Suðureyjar (5),Vestureyjar (6), West-Fiords (7), Drangar (8), Drangavík (9), Málmey (10), Ófeigsfiord (11) ,Skagi (12), Vatnsnes (13), Þaraláturs nes (14), Northeast-Coast (15), East-Coast (16), Skeidarársandur (17), Skógarsandur (18), Surtsey (19), Vigur (20).*

harbour seal is the only other seal species that breeds on the Icelandic coast. They are more numerous than grey seals and competition for space is quite noticeable in Iceland. In areas where grey seals move in to occupy haul-out sites in order to breed or moult, common seals will often move away. There is some anecdotal evidence that grey seal males kill common seal pups (various seal-hunters pers. comm.). These 2 seal species could also compete for cod (*Gadus morhua*) and other gadoids, which they both prefer (Hauksson and Bogason 1997). However, seasonal differences in life histories of these 2 species serve to reduce the overlap in the timing of foraging activity. Hooded seals (*Cystophora cristata*) are also seen in northern Icelandic waters and may compete with grey seals for cod (Hauksson and Bogason 1997, Thórdarson 2004). It is unlikely that grey seals are competing with whales for food; the most likely candidates are the toothed whales and the minke whale (*Balaenoptera acutorostrata*), which feed on fish to some extent (Sigurjónsson and Hauksson 1994, Sigurjónsson *et al.* 2000, Víkingsson and Galan unpublished). Harbour porpoises (*Phocoena phocoena*) feed mainly on capelin and sand eels (Víkingsson *et al.* 2003) and killer whales (*Orcinus orca*) feed presumably on herring (*Clupea harengus harengus*), which is not common in the diet of grey seals in Icelandic waters. However, killer whales are the main predator of seals in Icelandic waters, and it is likely, that killer whales have a greater impact on grey seals through predation, rather than competition (Sigurjónsson *et al.* 1988).

Early efforts to evaluate grey seal abundance in Iceland were based on catch statistics and anecdotal information from farmers who also hunted seals in the coastal regions (seal farmers). Seal farmers on the northwest coast of Iceland indicate that seal numbers increased substantially from only a few in 1940-50, to much higher numbers thirty years later (Jón Benediktsson Höfnum deceased and Pétur Guðmundsson, Ófeigsfirði, personal communication). In Breidafiord, West Iceland, data for the years 1966-71 indicate annual catches of 276-517 grey seal pups. Based on these catch levels, the population probably numbered at least about 2,000 animals (Arnlaugsson 1973). On the southeast-coast there were observations of large numbers of grey seals (500-1000), both pups and adults, during the first part of the twentieth century (Einarsdóttir 1995).

From 1980 to 2004, a series of surveys were undertaken to estimate grey seal pup production in Iceland. Here I present the results from these surveys and comment on changes in grey seal abundance in Iceland over that period of time.

MATERIALS AND METHODS

Surveys

The coast was divided into 7 coastal areas, where a total of 20 breeding colonies have been identified (Fig. 2). At some colonies, observers walked through the colonies and noted the num-

bers of pups, but at most, surveys to count pups were flown at an altitude of 100-300 feet using a high-winged Cessna-Skyhawk airplane during the fall of 1980, 1982, 1985, 1986, 1988, 1989, 1990, 1992, 1995, 1998 and 2002. Surveys flown in 1980, 1985, 1988 and 1989 were not successful owing to bad weather. In 1989, 2003 and 2004 multiple counts per autumn were performed on different parts of the coast. In most surveys, 2 observers counted, one in the front seat sitting with the pilot and one in the backseat. In the surveys of 1992, 1995, 1998, and 2002 and in the 2003 partial survey, only 1 observer counted, with help from the pilot. Animals were counted using a manual counter and total numbers were recorded on a portable tape-recorder. Large pup colonies were photographed using 400 ASA colour 35 mm slides, in a camera with an automatic aperture setting, an 80-150 zoom lens and 1/500 film-speed. Pups were counted from the slides using a binocular microscope, or by projecting the slides onto a white board.

Correction for undercounting, natural mortality and catch before the day of census

In some areas, hunting occurred prior to the survey. Estimates of pup production at these sites were obtained by adding in catch data from hunters to the pup counts obtained from the aerial surveys.

During the overflights, not all pups were visible, which would result in underestimation of pup production at the individual colonies. Counts were adjusted for missed pups, using a correction factor derived by comparing the aerial counts with independent shore counts using a $\Sigma a \cdot g / \Sigma a^2$, where g was total number of pups seen on land and a was total number of pups seen on the same site from the air. Counts were also corrected for natural mortality during the breeding season. Mortality information was obtained by visiting individual colonies and noting the numbers of dead pups. A mean mortality rate was estimated by averaging mortality rates for the individual colonies. Confidence limits were estimated assuming a log-Normal distribution. The correction factor for missed pups and mortality were then combined into 1 conversion factor (q). This was applied to the pup counts to determine numbers of animals present at the time of the survey.

Estimating breeding time and pup-production

In part of Frameyjar, West Iceland, and on the South and the northwest coast, 3 or more censuses were made during the autumns of 1989, 2003 and 2004 (Fig. 2). During ground counts, pups were classified into stages based on a combination of pelage colouration (indicative of moulting stage) and body shape as described by Bowen *et al.* (2003). The birth ogive was reconstructed by fitting the distribution of births to a normal, lognormal, log-logistic, weibull or gamma distribution using a log-likelihood to evaluate the fit (Radford *et al.* 1978, Lorentsen and Bakke 1995, Bowen *et al.* 2003). Birth ogives were derived by pooling data from all colonies. Correction factors were then applied across colonies depending on the date that each colony was surveyed. Total pup production (p) was estimated by dividing the number of observed births by the value of the area under the probability density curve, between the first and the last day of observations. This produced a proportion of total pupping completed when the survey was flown. Aerial survey counts were also corrected for pups leaving the breeding site by assuming that time spent onshore could be described by a normal distribution with a mean residency period of 22 days.

Estimating trend in the pup counts and statistical analyses of data

For estimating trends in pup-counts in each colony, counts were ($\log_e + 1$) transformed, because values did not follow a normal distribu-

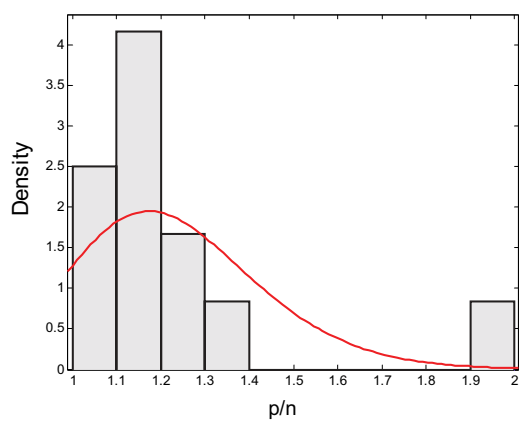

Fig. 3. *Distribution of p/n values from the staging of pups and the fitted lognormal probability density function to the observed values.*

Table 1. Comparison of counts of grey seal (*Halichoerus grypus*) pups made on land (G) and from the air (A), on the same locality. These counts were used to produce correction factor applied to aerial counts to account for missed pups in each region during aerial surveys.

Locality	Counts from air (A)		Counts on land (G)		G/A
	Day	Numbers	Day	Numbers	
Islands on the West-coast (6 on Fig.1)	12 Oct 1982	47	14 Oct 1982	49	1.04
Islands on the North-coast (12 on Fig. 1)	1 Nov 1982	75	6 Nov 1982	77	1.03
Surtsey, South-coast (19 on Fig. 1)1	15 Nov1998	17	15 Nov1998	30	1.76
Þaralátursnes, NW-coast (14 on Fig. 1)2	29 Oct 2004	1	29 Oct 2004	5	5
Overall ($[\Sigma G \bullet A]/[\Sigma G^2]$)					1.06

tion. This made it possible to evaluate the rate of change (r_s), in relation to the number of years of surveys completed since the reference year 1981, and number of days (d) from peak pupping date, by using a General Linear Model.

To calculate trends in pup production, estimates corrected for harvests prior to surveys, mortality and pups missed in surveys, in each coastal area and on the whole coast in relation to years. Counts were $\log_e$ transformed and analysed with a robust regression using interactive reweighted least squares (Hocking 2003). This approach minimizes the effect of outliers and extreme cases on the data, and is useful when outliers cannot reasonably be excluded. Differences in the timing of pupping between colonies and between years were investigated using analyses of covariance. Correlation between peak breeding dates and years were investigated separately at Frameyjar, Breidafiord. Statistical analyses were carried out using MATLAB® version 7.

RESULTS

Independent counts of pups were made within 5 days of a survey on 4 occasions on a rocky shore in Breidafiord and islands on the North coast in 1982, on 15 November 1998 on Surtsey and in the autumn of 2004 on Þaralátursnes (Table 1). An overall coefficient of 1.06 was calculated from the ratio of aerial pup counts to ground counts.

At 13 sites, a total of 6 dead pups were found amongst 282 living. This would indicate a natural mortality of pups (m) of about 2% (95% CI 1% – 4%) from birth to weaning. The correction factors for missed pups and mortality were combined into 1 conversion factor (q) of 1.08 (95% CI 1.07 - 1.10). This was applied to the pup counts to determine numbers of animals present at the time of the survey. Pupping was first observed in Surtsey, south Iceland on 13 September and in Faxa Bay and Breidafiord, west Iceland, on 16 September 1989 (Fig. 2). The latest new-born (<3 days old, 1st stage) pups detected (n = 2) were observed on 25 November 2000 on Skeiðarársandur. Peak pupping occurred around 14 October, day 44 (SE 3.13) (Table 2). There were significant differences in the timing of pupping between colonies, (P= 0.04). Breeding in Hvalseyjar, Faxa Bay in western Iceland was significantly earlier (P= 0.04), while breeding in Vigur and Surtsey, on the south coast of Iceland was significantly later than 14 October (P= 0.02). Although sample sizes are limited, the timing of peak pupping appears to be occurring later in the fall with a shift from 27 September (day 27) in 1990 to 4 October (day 34) in 1998, and finally 10 October (day 40) in 2003 in Frameyjar, Breidafiord, in west Iceland (see Table 2) (r = 0.97; P= 0.056). This is in accordance with observations by seal hunters over the period 1980-2003 (Hafsteinn Guðmundsson Flatey pers. comm.).

A significant negative annual trend in the number of pups was observed in Hvalseyjar (24%), in Tjaldurseyjar (14%) and in Skeiðarársandur (10%). Colonies along the other coastal areas did not show significant changes in the number of observed pups in relation to year, but in Frameyjar, Drangavik and Skeiðarársandur, there was a significant negative relationship between the number of pups observed and the number of days between the timing of the survey and the estimated period of peak pupping (Table 3).

Where possible the proportion of pupping that had been completed when the survey was flown was calculated on a colony by colony basis. At

some colonies, only 1 or 2 visits were possible to determine the proportion of animals in the different stages. The proportion of pups born for the entire Iceland population was estimated by combining all stage data. A lognormal distribution provided the best fit to the resulting pupping ogive, with a mean of 1.22 (SD = 0.045; log-likelihood 2.330) (Fig. 3). This was subsequently applied to the pup counts to correct for pups born after the surveys were flown (Table 2).

At 4 breeding sites on the south and west-coast, pup-production (p) was estimated directly from staging pups or multiple aerial surveys, during 2 or more years (Table 2). At Surtsey off the south coast, pup production data from 2 surveys indicate that trend in pup production increased by 3%; in Vigur on the southeast coast, pup production decreased by 12% (95% CI 1% - 24%) (P = 0.04; N = 4) according to a robust linear regression on $\log_e(p)$ on years and in Skeiðarársandur on the south-coast trend in pup production decreased by about 14% (95% CI 2% - 26%) between 1989 and 2003.

An analysis by coastal region using robust regression of $\log_e$(pups) showed a significant downward slope in Faxa Bay (r_s = -0.19, P = 0.01) and on the south coast (r_s = -0.08, P = 0.02). In other coastal areas no significant change occurred in relation to year, during 1982-2002 (Table 4).

The robust regression of $\log_e$(total number of pups) corrected for mortality and catches prior to counting on year (Table 5) gave a significant downward trend, r_s = -0.03 (±0.01 SE, P = 0.03), indicating that the total number of pups had decreased by about 3% (±1% SE, P = 0.03) annually, during the period 1982-2002. During the period 1990-2002, this downward trend doubled to -6% (±1% SE) annually (r_s = 0.11; P = 0.01).

DISCUSSION

Weather plays an important role in the ability to successfully complete surveys in Iceland. In this study, 4 out of 11 aerial surveys were incomplete resulting in limited data. Furthermore, counting animals at different sites each year is not advisable, because of anecdotal evidence for movements between coastal areas, related to exploitation and disturbance. In the autumn of 2004, when pup production was at its all time low in the northwest part of the coast, an increased number of pups were observed at some breeding sites in Vestureyjar, Breidafiord (Hafsteinn Guðmundsson pers. comm). Also, site fidelity may not be as strong in an exploited population as in a protected one, and dispersal of animals has been observed following hunting and marking operations (Summers *et al.* 1975, Pomeroy *et al.* 2000).

In spite of the application of factors to correct for pups missed by observers, mortality and births occurring after surveys were flown, these estimates are likely to underestimate grey seal pup production. One reason for this is that small groups of seals may be overlooked, especially when only 1 census of a colony is made. Also, animals may disperse from the colony before counting has been completed, resulting in an underestimate of total pup production at that colony (Lorentsen and Bakke 1995). This was particularly evident in some of our surveys, where up to 25 days separated consecutive flights and some animals had dispersed from the colonies. Finally, we may have underestimated natural mortality rates because dead pups disappear quickly, some being washed away to sea while others are trampled in the mud or dismembered by gulls, which would have led to an underestimate of total pup production. In this study, the observed mortality of around 2% is very low compared to that from studies completed in other areas (Bowen *et al.* 2003).

There appears to have been some change in the distribution of grey seals around Iceland since the 1950s, following a likely increase in the size of the grey seal population at that time. Animals began to spread north from the west coast to the northwest coast (Strandir and Skagi), and later to Drangey and Málmey, and as far as Melrakkaslétta on the northeast coast of Iceland. In 1995, when pups were found in these areas, the breeding distribution of grey seals covered nearly the whole Icelandic coast, with the exception of Melrakkaslétta to Stöðvarfiord (Fig. 2). However, no pups were observed there in 1998 and 2002. This early expansion between the 1950s and 1995 was likely a result of people leaving farms and moving into cities, which resulted in a reduction in disturbance and harvesting pressure. More recently there has been a reduction

Table 2. Peak pupping date and 90% confidence interval births for the Icelandic grey seal population (*Halichoerus grypus*), and information for estimation of the relationship between, pup counts on breeding sites (n), estimated pup production (p) and the correction factor to correct pup counts. [*=only part of Frameyjar; **=only part of Frameyjar but not the same as *; ***=only partly but the same part each time]

Breeding site (no on Fig. 2)	Date	Max count (n)	Breeding (Time interval for 90% births)	Pup-production (p)	p/n	Method, the distribution that gave best fit (log likelihood value)
Eyjar, NW-Coast	9 Nov 2000	8	18 Oct (8-28 Oct)	11	1.34	Staging lognormal (-24.92)
Eyjarey, NW-Coast	28 Oct 2001	22	16 Oct (7-26 Oct)	23	1.06	Staging normal (-69.62)
Frameyjar, W-Coast (3)*	6 Oct 1990	75	27 Sept (15 Sep-7 Oct)	78	1.04	Staging weibull (-252.53)
Frameyjar, W-Coast (3)**	2 Sept &16 Nov 1998	69	4 Oct (20 Sept-18 Oct)	79	-	2 aerial counts normal (-279.08)
Frameyjar, W-Coast (3)**	15 Sep-20 Nov 2003	207	10 Oct (15 Sep-6 Nov)	327	-	4 aerial counts weibull (-1288.46)
Hvalseyjar, W-Coast (1)	8 &14 Oct 1990	118	18 Sept (10 Sep-1 Oct)	131	1.11	Staging lognormal (-378.03)
Vestureyjar, W-Coast3 (6)	14 Oct & 6 Nov 1982	116	-	182	-	Total count
Vestureyjar, W-Coast3 (6)	22 Oct 2001	7	8 Oct (25 Sep-24 Oct)	9	1.29	Staging lognormal (-24.63)
Skeiðarársandur, S-Coast (17)	14 Sep-13 Dec 1989	358	27 Oct (17 Oct-7 Nov)	422	-	4 aerial counts log-logistic (-1469.25)
Skeiðarársandur, S-Coast (17)	7 & 21 Oct, 12 Nov & 15 Dec 1993	121	-	272	-	Total count
Skeiðarársandur, S-Coast (17)	7 Oct-15 Dec 1993	121	21 Oct (2 Oct-15 Nov)	267	-	4 surveys on foot lognormal(-928.19)
Skeiðarársandur, S-Coast (17)	7 & 21 Oct, 12 Nov & 15 Dec 1993	121	15 Oct. (27 Sep-7 Nov)	238	1.97	Staging gamma (-911.61)
Skeiðarársandur, S-Coast (17)***	22 Oct 1995	25	10 Oct (27 Sep-21 Oct)	27	1.06	Staging weibull (-84.79)
Skeiðarársandur, S-Coast (17)	1-19 Oct 1997	69	-	95	-	Total count
Skeiðarársandur, S-Coast (17)	1- 19 Oct 1997	62	12 Oct (28 Sep-23 Oct)	62	-	4 surveys on foot weibull (-215.65)
Skeiðarársandur, S-Coast (17)	1 - 19 Oct 1997	69	30 Sep (20 Sep-16 Oct)	79	1.16	Staging lognormal(-238.03)
Skeiðarársandur, S-Coast (17)***	29 Oct 1998	6	13 Oct (30 Sep-29 Oct)	7	1.16	Staging gamma (-21.51)
Skeiðarársandur, S-Coast (17)***	29 Oct 2002	18	12 Oct (29 Sep-27 Oct)	21	1.17	Staging lognormal (-63.32)
Skeiðarársandur, S-Coast (17)	17 Sep-11 Dec 2003	53	13 Oct (27 Sep-1 Nov)	69	-	6 aerial counts gamma (-260.42)
Surtsey, S-Coast (19)	14 Sep-13 Dec 1989	35	19 Nov (7 Nov-1 Dec)	38	-	4 aerial counts normal (-129.36)
Surtsey, S-Coast (19)	17 Sep-11 Dec 2003	37	20 Oct (25 Sep-28 Nov)	54	-	5 aerial counts gamma (-230.98)
Tjaldurseyjar, W-Coast (2)	16 Sep & 15 Oct 1997	7	6 Oct(13 Sep-30 Oct)	15	-	2 aerial counts normal (-40.09)
Vigur, S-Coast (20)	14 Sep-12 Dec1989	82	11 Nov (20 Oct-2 Dec)	141	-	4 aerial counts normal (-506.31)
Vigur, S-Coast (20)	18 Nov 1999	54	7 Nov (21 Oct-18 Nov)	61	1.14	Staging weibull (-192.48)
Vigur, S-Coast (20)	31 Oct 2002	20	8 Oct (30 Sep-17 Oct)	24	1.21	Staging log-logistic (-61.73)
Vigur, S-Coast (20)	17 Sep-11 Dec 2003	13	4 Nov (3 Oct-4 Dec)	26	-	5 aerial counts weibull (-110.55)
Strandir, NW-Coast (8,9,11 and 14)	27 Sep-18 Nov 2004	68	20 Oct (24 Sep-13 Nov)	121	-	3 aerial counts weibull (-458.37)

Table 3. Pup-counts (the maximum if more than 1 value was available) at 17 breeding sites of the Icelandic grey seal, with yearly rate of change since 1981 (Years), rate of change in (Days), the influence of the interval in days from peak breeding on the counts and overall deviation from a GLM analyses of $\log_e$(pups+1) (see Table 2, ns not significant, *, **, *** significant at the 5, 1 and 0.1% level respectively).

Breeding site (No)	1982	1985	1986	1988	1989	1990	1992	1995	1998	2002	Years	Days	Deviation
Hvalseyjar (1)	225	96	145	-	39	152	108	24	3	4	-0.24**	-0.05ns	2.64
Tjaldurseyjar (2)	57	35	49	-	12	57	30	27	2	6	-0.14*	-0.02ns	3.10
Frameyjar (3)	178	62	112	-	801	226	132	173	155	167	-0.05ns	-0.08*	4.83
Skálmarnes (4)	15	2	64	-	162	147	262	208	144	72	0.02ns	-0.06ns	28.52
Suðureyjar (5)	17	5	16	-	7	12	11	2	15	2	-0.07ns	-0.01ns	2.86
Vestureyjar (6)	273	73	452	-	341	304	299	364	118	84	-0.03ns	-0.06ns	14.35
Drangar (8)	257	-	104	32	-	479	103	105	118	223	0.02ns	0.04ns	8.88
Drangavík (9)	30	-	50	34	-	10	26	3	10	40	-0.03ns	-0.13*	2.38
Málmey (10)	0	-	0	0	-	5	0	2	0	9	-	-	-
Ófeigsfiord (11)	13	-	20	2	-	98	54	62	70	53	0.04ns	0.09ns	6.07
Skagi (12)	108	-	62	-	-	67	51	115	35	28	-0.04ns	-0.03ns	3.64
Vatnsnes (13)	0	-	10	3	-	4	5	14	0	14	-0.05ns	-0.02ns	7.63
Þaralátursnes (14)	40	-	11	19	-	33	60	40	129	18	0.02ns	-0.03ns	5.92
Skeidarársandur (17)	294	506	276	287	358	258	212	112	96	72	-0.10***	-0.05***	3.22
Skógarsandur (18)	0	12	0	-	0	40	1	1	0	0	-0.07ns	-0.04ns	9.92
Surtsey (19)	0	-	25	8	73	23	25	39	30	35	0.07ns	-0.03ns	10.07
Vigur (20)	3	80	50	7	83	46	35	21	18	24	-0.03ns	-0.07ns	5.56

Table 4. Total number of pups on the coastal areas of Iceland where grey seals (*Halichoerus grypus*) breed. r_s is estimated trend of $\log_e$(pups) with time (years from 1981), using robust regression. Counts are not corrected for mortality or pups that may have been born after the survey was completed. Robust s is an estimate of the standard deviation of the error term, s = MAD/0.6745 (MAD mean absolute deviation; Hocking 2003).

Coastal Area	1982	1986	1989	1990	1992	1995	1998	2002	r_s ±SE	Robust s, p
Faxa Bay	282	194	51	209	138	51	5	10	-0.19 ±0.05	0.86, 0.01
Breidafiord	483	644	590	689	704	747	432	325	-0.02 ±0.02	0.30, 0.27
Westfiords (7)	0	16	3	14	9	6	15	0	-	-
NW	448	257	-	696	299	341	362	385	-0.003 ±0.02	0.37, 0.89
NE and E (15 & 16)	0	0	-	0	0	11	0	8	-	-
South	297	351	514	367	273	173	144	131	-0.08 ±0.02	0.41, 0.02
Catch before surveys	268	200	-	42	34	163	122	47	-	-
Total	1,778	1,662	-	2,017	1,457	1,492	1,080	906	-0.03 ±0.01	0.19, 0.03

Table 5. Total pups counted on the coast, from Table 4, corrected for undercounting and catch (conversion factor q + catch prior to date of counting). Estimated pup-production for the Icelandic grey seal, in years when counting was achieved in all coastal areas, C_{corr} multiplied with p/n (1.21 log-normally distributed with variance 0.045; log-likelihood 2.330), 95% confidence interval are in parentheses.

Year	1982	1986	1990	1992	1995	1998	2002
Counted pups (C)	1,510	1,462	1,975	1,423	1,329	958	859
Missed pups by observers, and mortality (C*q)	121 (106-151)	117 (102-146)	158 (138-200)	114 (100-142)	106 (93-133)	77 (67-96)	69 (60-86)
Corrected total number of pups, catch before days of counting included (C_{corr})	1,899 (1,884-1,929)	1,779 (1,764-1,808)	2,175 (2,155-2,214)	1,571 (1,556-1,599)	1,598 (1,585-1,625)	1,157 (1,147-1,176)	975 (966-992)
Pup-production (C_{corr}*p/n: 1, 1.21, 1.60)	2,298 (1,884-3086)	2,153 (1,764-2,892)	2,632 (2,155-3,542)	1,901 (1,556-2,558)	1,934 (1,585-2,600)	1,400 (1,147-1,882)	1,180 (966-1,587)

in the number of breeding colonies used by grey seals, as well as a reduction in grey seal pup production around Iceland, as a result of increased harvesting around the island. Currently, the main breeding colonies of grey seals are limited to the southeast and northwest part of the coast. Given the reduction in pup production, total population size has likely also decreased. Observations indicate that during the moult in March-May and during periods outside of the moulting and breeding season, grey seals are distributed all around the Icelandic coast. The majority of the population is thought to occur off the west, northwest and southeast coasts, but distribution at this time is poorly documented.

Grey seals are hunted in almost every part of the Icelandic coast. Only Surtsey is totally protected. The change in the breeding distribution may mirror dispersal of first an increasing and then declining population, but the abandonment of certain colonies might also be in response to harvesting in these areas either directly through population reduction or indirectly through abandonment of sites due to disturbance (Summers and Harwood 1978, cited in Harwood 1981).

In Iceland, the pupping season has traditionally been considered to occur from the middle of September to early November, with a maximum in mid-October. According to seal farmers, pupping along the northern coast occurs about month later, which is supported by our information on the seasonal distribution of pupping. The timing of pupping in Iceland is similar or slightly earlier than that of grey seals in the British Isles (Bonner 1976).

Some inter-annual variation in the timing of births was observed. Icelandic seal hunters believe that this variability is caused by a combination of weather and tide conditions. Pupping occurs later now than in 1980, according to seal farmers in Breidafiord. That is partly confirmed in this study, in one part of Breidafiord. This delay in breeding may be due to environmental conditions or may be a response to harvesting at the breeding sites. Pups of late breeding females tend to survive, while pups from early and average breeding females have a greater chance of being taken by hunters.

Early attempts to estimate grey seal pup abundance around Iceland consisted of single surveys. Owing to the extended duration of the grey seal breeding season it was recognized that these counts were underestimates because of births occurring after surveys were flown. In other areas, multiple counting surveys of all known pupping colonies are completed, and corrections are applied to the estimates to take into account animals born after surveys have been flown, or for animals that may have left the pupping site before surveys are completed (Duck and Thompson 2007). An alternative approach developed in North America utilizes a single counting survey, and then multiple stage determination surveys to model the distribution of births and develop correction factors to apply to the survey counts (Hammill *et al.* 2007). Owing to financial and logistical difficulties, correction factors in this study were developed at only a few whelping colonies around the Iceland coast. These correction factors were combined and applied to all colonies to estimate pup production in Iceland. This ratio varied from 1.04 to 1.97 with a mean value of 1.21 (Table 2), which is a little higher than a factor of 1.16-1.20, that has been used for the British grey seals), but falls within the range of correction factors of 1.07 to 1.61 that have been applied to Northwest Atlantic grey seals on Sable Island (Harwood *et al.* 1991, Bowen *et al.* 2003).

Pup counts can be good indicators of abundance in populations with stable age distributions. If the age distribution is changing due to ecosystem changes or other factors, pup counts will not be a good indicator until the population reaches a new stable age distribution (Berkson and DeMaster 1985). In a harvested, declining population of grey seals, one can hardly expect a stable age distribution unless the harvesting of each age-class, of males and females, is proportionally the same every year (see Harwood 1981). In this study, grey seal pup production was evaluated around the coast of Iceland. However, in many cases managers and stakeholders are more interested in estimates of total abundance. Such an estimate requires more detailed information on age specific reproductive and mortality rates and removals from the population. Rough estimates might be possible using adult to pup ratios obtained in other studies. Such ratios may vary from 3.5 to 5.4 adults to pups (Hewer 1964, Mansfield and Beck 1977, Haug *et al.* 1994, Hammill *et al.* 1998, Stobo and Zwanburg 1990). Applying such ratios to grey seal pup counts in Iceland would result in a population of 8,000-11,500 animals in 1982, declining to 4,100 to 5,900 animals in 2002.

Using catch statistics, Arnlaugsson (1973) estimated that there were at least 2,000 grey seals in the west area during the 1960's. Although there are no catch statistics available from other parts of the coast, if we assume that similar numbers of animals were breeding around the coast then a minimum estimate for the number of grey seals around Iceland during that period would be on the order of about 4,000 to 5,000 grey seals, equally divided between the west coast and southeast coast of Iceland. It appears that the population increased from the 1960s until 1982, but then has decreased again due to an increase in hunting effort. Declines in pup production have occurred in 2 coastal areas of Iceland. Overall the Icelandic grey seal population has likely decreased by about 3% (95% CI 1% - 5%) annually from 1982 to 2002. After 1990 the rate of population decline was probably more rapid at about of 6% per year.

This study indicates that there has been a marked decline in grey seal abundance in Icelandic waters since the mid-1990s. Anecdotal observations from seal hunters also support these findings. Furthermore, there has been a reduction in the distribution of breeding colonies around the country, with grey seals now limited for the most part to the northwest and southeast coasts. In recent years, catches have

also declined (MRI 2005), probably due to the smaller grey seal population. Because of its current low number, this population should be monitored more frequently, preferably annually, by a minimum 3 aerial surveys per site within the breeding season or alternatively using ground counts at the larger colonies, in order to have sufficient power in the survey dataset to detect small but significant changes in the population (Galimberti 2002). In 2004, the Icelandic Government developed a specific management objective for the Icelandic grey seal population, which aims to maintain the resource.

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