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Original Article

From pup production to quotas: current status of harp seals in the Greenland Sea

Tor Arne Øigård*, Tore Haug, and Kjell Tormod Nilssen

Institute of Marine Research, PO Box 6404, NO-9294 Tromsø, Norway

Corresponding Author: tel: +47 77 60 97 30; fax: +47 55 23 85 31; e-mail: tor.arne.oeigaard@imr.no

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Harp seals (*Pagophilus groenlandicus*) have been harvested for centuries in the North Atlantic. Estimating abundance and monitoring changes in population size are critical for the management of the species. In March 2012, the harp seal pup production was estimated from aerial photographic surveys over the whelping areas. A total area of 305 km^2 was photographed and 6034 pups were counted on the photos. From this the total pup production estimate was 89 590 (s.e. = 12 310, *CV* = 13.7%). The status of the stock was subsequently assessed by fitting a population model to the independent pup production estimate, the historical catch data, and the historical reproduction data. The 2013 total abundance (including pups) was estimated to be 627 410 (95% *CI* = 470 540–784 280) harp seals. We demonstrate how the model is used in assessment when exploring the effect of various catch scenarios on future predictions.

Keywords: abundance estimation, aerial photos, age-structured population model, harp seals, management, pup production.

Introduction

Three stocks of harp seals (*Pagophilus groenlandicus*) inhabit the North Atlantic Ocean (Sergeant, 1991). Whelping occurs in Canadian waters (the Northwest Atlantic stock), off the east coast of Greenland (the Greenland Sea or West Ice stock), and in the White Sea (the Barents Sea/White Sea stock). The Greenland Sea stock has been subject to commercial exploitation for centuries (Iversen, 1927; Nakken, 1988; Sergeant, 1991). Exploitation levels reached an historical maximum in the 1870s and 1880s when Norwegian annual catches of harp seals (pups and adults) varied between 50 000 and 120 000—in addition, several other nations hunted an unknown number of animals (Iversen, 1927; Rasmussen, 1957). It was evident that the catch levels in the 1870s were higher than the stock could sustain, and some regulatory measures (mainly designed to protect adult females) were taken in 1876 (Iversen, 1927). In the first decades of the 20th century Norway was the only hunting nation in the area, and the harp seal catches varied between 10 000 and 20 000 animals, but increased to around 40 000 seals annually in the 1930s (Iversen, 1927; Rasmussen, 1957; Sergeant, 1991). After a 5-year pause in the sealing operations during World War II, total annual catches quickly rose to a post-war maximum of about 70 000 in 1948, but then followed a decreasing trend until quotas were imposed in 1971 (Sergeant, 1991; ICES, 2011). From 1955–1994 a minor part of the catches was taken by the Soviet Union/Russia, and the total annual catches varied from a few hundred in 1971 to ~17 000 in recent times (ICES, 2011).

Available knowledge of both the previous and present abundance of Greenland Sea harp seals is rather restricted. As judged both from catch per unit effort (cpue) and mark–recapture analyses of pup production abundance, it has been assumed that the stock has increased ever since the early 1960s, but evidence of the level of increase has been rather imprecise (Ulltang and Øien, 1988; Øien and Øritsland, 1995). During the period 1977–1991, about 17 000 harp seal pups were tagged in a comprehensive mark–recapture experiment in the Greenland Sea (Øien and Øritsland, 1995). From this experiment, a pup production of 40 000–50 000 was estimated in 1980. By modelling, the 1988 pup production was projected to have been within the range of 53 000–69 000, which would imply a stock of one-year-old and older (1+) animals within a range of 230 000–290 000 (Ulltang and Øien, 1988). Updates to the mark–recapture-based pup production estimates indicated a pup production in 1991 of 67 300 (s.e. = 5400, *CV* = 8.0 %) (ICES, 2001). Results from aerial surveys suggested a minimum pup production in 1991 in excess of 55 000 (Øritsland and Øien, 1995). New aerial surveys conducted 11 years later (in 2002, see Haug *et al.*, 2006) yielded an estimate of 98 500 (s.e. = 16 800, *CV* =

17.0%), whereas the most recent estimate in 2007 was 110 530 (s.e. = 27 680, $CV = 25\%$) (Øigård *et al.*, 2010).

Current management of Greenland Sea harp seals is based on assessments performed by ICES (see ICES, 2011). Population assessments are generally based on a population model that estimates the current total population size, incorporating historical catch data, estimates of pup production, and historical values of reproductive rates. These estimates are then projected into a future population size for which statistical uncertainty is provided for several relevant catch options.

The aim of this paper is to give an overview of the methods used in providing scientific advice regarding the Greenland Sea harp seal population. A procedure for estimating the pup production is presented. A recent pup production survey (carried out in March 2012) is described in detail, and the results from the survey are presented. The status of the stock has subsequently been assessed by fitting a population model to the pup-production estimates. The model is described in detail, and we demonstrate how the model can be used in exploring the effect of future model predictions under various catch scenarios.

Material and methods

Pup production survey

Logistics

An ice-strengthened expedition vessel with a helicopter platform and an Ecureuil AS 350 B1 helicopter was used for reconnaissance and pup age-staging surveys in the Greenland Sea drift ice. Two fixed-wing twin engine Piper Navajo aircraft were used for reconnaissance and photographic surveys. The aircraft were mainly based at Constable Pynt (Nerlerit Inaat) airport (50 km north of Scoresbysund, East Greenland), but the airport in Akureyri (Iceland) was also used.

Reconnaissance surveys

In 2012 the ice cover was close to the East Greenland coast, and aerial reconnaissance surveys aimed at finding whelping seal patches were carried out in areas historically used by harp seals in the Greenland Sea (Figure 1). Survey altitudes were 160–300 m.

Due to ice drift and period of pupping (mid to late March, see Øritsland and Øien, 1995; Haug *et al.*, 2006; Øigård *et al.*, 2010), most areas were surveyed repeatedly to minimize the chance of missing whelping concentrations. Colour markers, VHF transmitters and two satellite-based GPS beacons were deployed in the major whelping concentration areas to facilitate relocation and to monitor ice drift (see Figure 1).

Helicopter reconnaissance flights were flown between 18 and 21 March in areas between 72°05'–74°00'N and 14°16'–16°51'W, and on 1 April between 69°15'–69°50'N and 17°43'–19°40'W as repeated systematic east–west transects from the ice edge in the east into more denser drift ice in the west (Figure 1.) The lengths of transects were approximately 10–30 nautical miles, and they were usually spaced 5 nautical miles apart, modified according to the actual ice configurations during the surveys.

The fixed-wing aircraft had the capacity to conduct reconnaissance surveys that covered larger areas than the helicopter surveys, and were used to cover potential seal whelping areas along the edge of the drifting ice from 74°10'N 12º00'W in the northeast to 67°55'N 23 º45'W in the southwest (Figure 1). These surveys were usually flown at altitudes of ~180 m, but also at lower altitudes in short periods due to low cloud base. Repeated systematic east–west transects (normally spaced 10 nautical miles apart) were

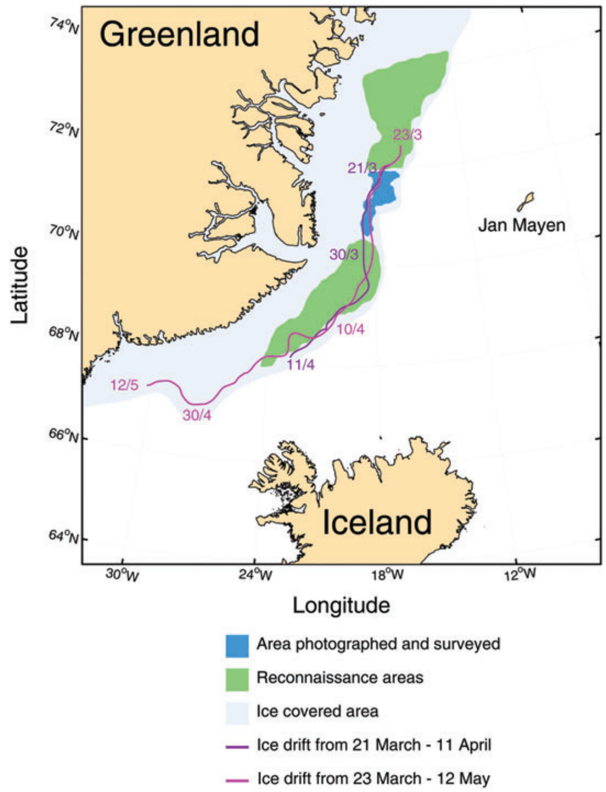

Figure 1. Area covered by photographic survey over whelping patches on 28 March (blue), and areas covered by reconnaissance flights conducted by aircraft (22 March – 1 April) and helicopter (18 March – 1 April) (green). Ice drift in the Greenland Sea during the period 21 March – 11 April (purple line) and 23 March – 12 May, as observed from two satellite-based GPS beacons deployed on the ice.

flown from the eastern ice edge and usually 20–30 nautical miles (sometimes longer) over the drift ice to the west. Transects were usually ended in the west when the ice conditions changed to become very dense, with no water between the ice floes and increased snow coverage on the ice. Along the eastern ice edge, some additional transects were also flown in order to cover tongues of drift ice stretching to the east.

Photographic surveys

The helicopter was used to define the geographic range of the whelping patches prior to the fixed-wing aircraft photo surveys. Both aircraft were equipped with Vexcel Ultracam Xp digital cameras, which provide multichannel images (Red Green Blue Infrared). The cameras were operated at an altitude of ~330 m for both harp and hooded seals, except for transects 26 and 27 (see Table 1) where the altitude was 250 m (AGL) due to fog. The photos covered 226 × 346 m and 170 × 260 m at altitudes of 330 m and 250 m, respectively. At 300 m height the camera resolution was 1.8 cm. Cameras were turned on when seals were observed on a transect line and turned off when the transect line ended at the eastern ice edge, or when no seals were observed for an extended period along the line to the west. East–west transect lines were flown with 3 nautical miles apart, and ~90% of the lines were photographed without overlapping photos.

Photographic counts

The digital photos were analysed by two experienced readers using Adobe Photoshop, and the positions of all pups were recorded

Table 1. East–west transects (spaced 3 nautical miles) flown during a fixed-wing photographic survey of harp seal whelping areas in the Greenland Sea drift ice on 28 March 2012.

Transects	Lat. N	Start Lon. W	End Lon. W	Photos taken	Pups counted
1	72.01	16.52	17.29	75	14
2	71.58	17.04	16.51	25	0
3	71.55	16.27	17.43	150	1
4	71.52	17.48	16.15	188	132
5	71.49	16.35	17.48	146	62
6	71.46	17.44	16.47	118	69
7	71.43	16.53	17.47	111	238
8	71.40	17.51	16.54	119	271
9	71.37	16.38	17.55	155	453
10	71.34	17.45	16.37	140	955
11	71.31	16.36	17.42	144	343
12	71.28	17.50	16.36	157	329
13	71.25	16.33	17.54	169	88
14	71.22	18.22	16.49	195	242
15	71.19	18.29	17.30	121	740
16	71.16	18.29	17.53	76	394
17	71.13	17.57	18.24	54	136
18	71.10	18.24	17.51	67	213
19	71.07	17.56	18.28	68	74
20	71.04	18.25	17.57	61	158
21	71.01	18.01	18.36	75	117
22	70.58	18.33	18.09	50	86
23	70.55	18.13	18.46	76	116
24	70.52	18.04	18.38	73	407
25	70.49	18.34	18.00	75	309
26	70.46	18.17	18.38	58	87
27	70.43	18.31	18.15	46	0
Sum				2 792	6 034

Number of photos and pups on the photos are presented.

manually on a digital overlay. A digital grid was used to aid in the systematic search of the images. After reading all photos, the readers re-read a series of their photos in sequence to determine if identifications had improved over the course of the readings. In general, the main challenge when reading this type of photo is to separate white pups from the background of white ice. The ice is not smooth, but has a bumpy surface with ice formations of various shapes. This creates shades and obstructions that can obscure the readability of the images. To correct for misidentified pups, a number of photos were selected from one reader and read by the other reader. Then the two readers compared their readings and agreed on the best estimate representing the true number of pups present on a photograph. We assumed that the true number of pups (***) was modelled by a linear regression model as $y_{j,k} = a + bn_{j,k} + u_{j,k}$, where $n_{j,k}$ is the counts of the kth photo in the jth transect, a is the estimated intercept, b is the estimated slope, and $u_{j,k}$ is a random component that is normally distributed with zero mean and standard deviation σ. Using the estimated parameters we applied a linear correction model for each of the original counts, i.e.

$$\hat{n}_{j,k} = a + bn_{j,k}. \quad (1)$$

The measurement error for each photo associated with predicting the best estimate follows naturally by:

$$V_{j,k}^{meas} = \sigma^2 + \mathrm{var}(a) + 2\mathrm{cov}(a, b)n_{j,k} + \mathrm{var}(b)n_{j,k}^2, \quad (2)$$

where var(a) is the variance of the intercept, var(b) is the variance of the slope, and cov(a,b) is the covariance between the intercept and the slope.

Estimation of pup abundance

The photographic surveys were based on a systematic sampling design with a single random start and a sampling unit of transects of variable length. The estimated number of pups on the ice at the time of survey may be written as (Salberg *et al.*, 2008; Øigård *et al.*, 2010):

$$\hat{N} = T\sum_{j=1}^{J} W_j x_j, \quad (3)$$

where $W_j = l_j/A_j$, A_j is the area covered of all photos on transect j, l_j is the length of transect j, J is the number of transects, and $x_j = \sum_{k=1}^{P_j} \hat{n}_{j,k}$ is the sum of the corrected counts on transect j. The number of photos on the jth transect is P_j and T is the spacing between transects in survey. This estimator takes into account changes in transect width along transects and between transects due to changes in flight height.

The estimates of error variance V^s, based on serial differences between transects were calculated as (Salberg *et al.*, 2008):

$$V^s = \frac{TJ}{2(J-1)}\left(T - \frac{\sum_{j=1}^{J} A_j}{\sum_{j=1}^{J} l_j}\right)\sum_{j=1}^{J-1}(W_j x_j - W_{j+1}x_{j+1})^2. \quad (4)$$

The variance associated with reading errors for the whole survey is then (Salberg *et al.*, 2008):

$$V^{meas} = T^2\left[\sum_{j=1}^{J} W_j^2 P_j \sigma^2 + \left(\sum_{j=1}^{J} W_j P_j\right)^2 \mathrm{var}(a) + 2\mathrm{cov}(a, b)\left(\sum_{j=1}^{J} W_j P_j\right)\left(\sum_{j=1}^{J} W_j \sum_{k=1}^{P_j} n_{j,k}\right) + \mathrm{var}(b)\left(\sum_{j=1}^{J} W_j \sum_{k=1}^{P_j} n_{j,k}\right)^2\right]. \quad (5)$$

To obtain the total sampling variance of the survey, the variance associated with the mis-identification corrections V^{meas} was added to the sampling variance V^s, i.e.

$$V = V^s + V^{meas}.$$

Estimating temporal birth distribution

To correct the estimates of abundance for seal pups that had left the ice or were not yet born at the time of the photographic survey, it was necessary to estimate the distribution of births over the pupping season. This was done using information on the proportion of pups in distinct age-dependent stages, as described for the northwest Atlantic harp seals by Stewart and Lavigne (1980) and later used for Greenland Sea harp seals by Haug *et al.* (2006) and Øigård *et al.* (2010). These arbitrary, but easily recognizable age categories were based on pelage colour and body condition, overall appearance, and muscular coordination. The various stages used were: Newborn, Yellow, Thin, Fat, and Grey. The mean duration of the various stages were obtained from Kovacs and Lavigne (1985) and Stenson *et al.* (2003). To determine the proportion of pups in each stage on a given day, random samples of pups were obtained by series of helicopter transects over the patch, just above the pups. The patches were covered with systematic east–west staging transects (spaced 3–5 nautical miles apart) on 20, 22, 23, 24, 27 and 29 March.

A full review of the method used to estimate the proportion of pups on the ice during the pupping season was given by Øigård *et al.* (2010).

Total pup production estimate

To correct for pups still not born, and pups that had left the ice at the time of the photographic survey, the estimated numbers of pups on the ice at the time of the survey were corrected by:

$$\hat{N}^{corr} = \frac{\hat{N}}{\hat{Q}}, \tag{6}$$

where $\hat{Q}$ is the estimated proportion of pups visible on the photographs at the time of the survey.

The estimates of N and Q are independent and therefore the error variance of the estimated total number of pups born in the patch $\hat{N}^{corr}$ may be obtained using the δ-method, i.e. (Casella and Berger, 1990):

$$V^{corr} = \left(\frac{1}{Q}\right)^2 V + \left(\frac{N}{Q^2}\right)^2 V^Q, \tag{7}$$

where V^Q is the estimated variance of $\hat{Q}$.

Stock assessment

Population model

The population model is an age-structured population dynamics model. It uses historical catch data, reproductive data, and estimates of pup production in order to estimate the current total population. Reproductive data and catch data used are found in ICES (2011). Pup production estimates are available from mark–recapture estimates (1983–1991; Øien and Øritsland, 1995; ICES, 2011) and aerial surveys conducted in 2002 (Haug *et al.*, 2006) and 2007 (Øigård *et al.*, 2010).

It is assumed that the population had a stable age structure in year $y_0 = 1945$, i.e.

$$N_{i,0} = N_{y_0} s_{1+}^{i-1}(1 - s_{1+}),\ i = 1, \ldots, A-1, \tag{8}$$

$$N_{A,0} = N_{y_0} s_{1+}^{A-1}. \tag{9}$$

Here A is the maximum age group containing seals aged A and more and selected to be 20 years (ICES, 2011), and N_{y0} is the estimated initial 1 + population size in year y_0. All catch data from the years prior to 1946 are unreliable—also, they do not separate between pups and older seals (Iversen, 1927; Rasmussen, 1957; Sergeant, 1991). In some years only total catches for the area (including both harp and hooded seals) were reported. This is the reason why we start our modelling in 1946, and why we do not attempt to run the model further back in time.

The model has the following set of recursion equations:

$$\begin{aligned} N_{1,y} &= (N_{0,y-1} - C_{0,y-1})s_0, \\ N_{a,y} &= (N_{a-1,y-1} - C_{a-1,y-1})s_{1+}, \quad a = 2, \ldots, A-1, \\ N_{A,y} &= \left[(N_{A-1,y-1} - C_{A-1,y-1}) + (N_{A,y-1} - C_{A,y-1})\right]s_{1+}, \end{aligned} \tag{10}$$

The survival probabilities s_0 and s_{1+} for the pups and1 + seals are determined by the natural mortalities M_0 and M_{1+}, respectively. The assumption that the mortality rate is age-independent within the 1+ seals is because available data do not allow for a more detailed age-dependence to be estimated. $C_{a,y}$ is the age-specific catch number. Catch records only provide information about the annual number of pups and number of 1+ seals caught. In the absence of information about age-specific catch numbers, we employ *pro rata* rules in the model (Skaug *et al.*, 2007):

$$C_{a,y} = C_{1+,y}\frac{N_{a,y}}{N_{1+,y}},\quad a = 1, \ldots, A, \tag{11}$$

where $N_{1+,y} = \sum_{a=1}^{A} N_{a,y}$ and $N_{a,t}$ is the number of individuals at age a in year y.

The modelled pup production is given by:

$$N_{0,y} = \frac{F_y}{2}\sum_{a=1}^{A} p_{a,y}N_{a,y}, \tag{12}$$

where $N_{a,y}/2$ is the number of females at age a in year y, F_y is the time-variant pregnancy rates, and $p_{a,y}$ are the time-variant maturity curves.

The model estimates the initial population size N_{y0} where y_0 is 1945. Also the mortalities M_0 and M_{1+} are estimated. The model is fitted to the survey pup production estimates.

Assuming normality for the pup production counts, their contribution to the log-likelihood function is:

$$\sum_y -\log(cv_{0,y}) - \frac{1}{2}\frac{(N_{0,y} - n_{0,y})^2}{cv_{0,y}n_{0,y}}, \tag{13}$$

where $n_{0,y}$ and $cv_{0,y}$ denote the survey pup production count and corresponding CV for year y. A normal prior is also assumed for the initial population size N_{y0}, and the mortalities M_0 and M_{1+}. The likelihood-contributions for these parameters are:

$$-\frac{1}{2}\left(\frac{N_{y_0} - \mu_{N_{y_0}}}{\sigma_{Ny_0}} + \frac{M_0 - \mu_{M_0}}{\sigma_{M_0}} + \frac{M_{1+} - \mu_{M1+}}{\sigma_{M1+}}\right) - \log(\sigma_{N_{y_0}}) - \log(\sigma_{M_0}) - \log(\sigma_{M1+}). \tag{14}$$

Here the μ's and the σ's are the mean values and the standard deviations of the normal priors used, and the values used are shown in Table 2.

Calculations and visualizations were done in R (R Core Team, 2012). All parameter estimates are found by minimizing the likelihood function using the statistical software AD Model Builder (Fournier *et al.*, 2012). AD Model Builder uses a quasi-Newton optimization algorithm with bounds on the parameters, and calculates estimates of s.e.'s of model parameters using the δ-method (Casella

Table 2. Estimated mean values and standard deviations of the parameters used in the model.

	Model estimates	
Parameters	**Mean**	**s.d.**
N_{y_0}	260 167 (900 000)	22 268 (900 000)
M_0	0.28 (0.24)	0.19 (0.2)
M_{1+}	0.11 (0.08)	0.02 (0.1)
$N_{0,2013}$	93 010	11 631
$N_{1+,2013}$	534 300	79 186
$N_{Total,2013}$	627 410	80 036

Priors used are shown in brackets.

and Berger, 1990). Normal priors were used on the unknown parameters, hence the model is of a Bayesian character. AD Model Builder also allows full Bayesian analysis via Markov chain Monte Carlo (MCMC) sampling (Gelman *et al.*, 1995).

Exploring catch options

ICES have developed a precautionary harvest strategy for the management of harp seals. The strategy includes two precautionary reference levels and one conservation (limit) reference level (see Hammill and Stenson, 2007). The reference levels relate to the pristine population size, which is the population that would be present on average in the absence of exploitation, or a proxy of the pristine population (which in practical terms is referred to as the maximum population size historically estimated from the population model, N_{max}). A conservation, or lower limit reference point, N_{lim}, identifies the lowest population size that should be avoided with high probability. The first precautionary reference level is established at 70% (N_{70}) of N_{max}. When the population is between N_{70} and N_{max}, various harvest levels could be used while aiming to keep the population above the N_{70} level. ICES (2008) has suggested that this could be done by designing the total allowable catch (TAC) to satisfy a specific risk criterion that implies a 0.8 probability of remaining above N_{70} over a 10-year period. When a population falls below the N_{70} level, conservation objectives are required to allow the population to recover to above the precautionary (N_{70}) reference level. N_{50} is a second precautionary reference point at which stricter control rules must be implemented, whereas the N_{lim} reference point, set by ICES (2008) at 30% (N_{30}) of N_{max}, is the ultimate limit point at which all harvest must stop.

The ICES management of harp seals requires that the populations in question are defined as "data rich". Data-rich stocks should have data available for estimating abundance in which a time-series of at least three abundance estimates should be available (spanning a period of 10–15 years with surveys separated by 2–5 years), and the most recent abundance estimates should be based on surveys and supporting data (e.g. birth and mortality estimates) that are no more than 5 years old. Stocks whose abundance estimates do not meet all these criteria are considered "data poor", and should be managed more conservatively. The Greenland Sea harp seal population is data rich, and predictions of the population trajectory have been explored under various catch scenarios. The following options were considered: (i) no hunt; (ii) current catch level; (iii) equilibrium catches level; and (iv) catches that would reduce the population to N_{70} with a probability of 0.8 over a 10-year period.

Current catch level is the average of the catches in the period 2008–2012. The equilibrium catch level is defined as the (fixed) annual catch level that stabilizes the future 1+ population under the estimated model. The catch level that would reduce the population size to N_{70} with a probability of 0.8 over a 10-year period is found by finding the catch level that has N_{70} just included in the 80% confidence interval of the 10-year prediction of the total population size.

Results

Pup production estimation

Identification of whelping areas

A small breeding patch, denoted Patch A, was observed during helicopter reconnaissance flights on 19 March between 73°00' and 73°18'N, and 14°28' and 15°05'W. To monitor ice drift and facilitate relocation, a satellite-based GPS beacon was deployed on the ice in this patch. During helicopter reconnaissance flights on 21 March a much larger harp seal whelping patch, denoted Patch B, was located between 72°00' and 72°25'N, and 15°30' and 17°00'W. A satellite-based GPS beacon and a VHF transmitter were also deployed in this patch. Subsequent helicopter staging flights in the two patches confirmed substantially increasing numbers of harp seals. The general drift of the two patches was in a southwesterly direction (Figure 1). Due to more open drift ice in patch A, this patch drifted faster than patch B. Thus, on 28 March the two patches had merged, yielding one large patch with one GPS beacon in each end. In size, the small patch was probably around 5% of the large patch when they merged.

On 29 March, both fixed-wing aircraft made new reconnaissance flights north of the photographed patches but observed no whelping seals. On 1 April some additional reconnaissance flights with helicopter and the two aircraft were conducted south of the photographed area. No pups or breeding seals were observed.

The ice drift varied in the survey period, but could be as much as 36 nautical miles per day in a south–southwesterly direction, as seen from the satellite-based GPS beacons deployed on the ice (Figures 1 and 2). During the survey period the ice drift was up to 25 nautical miles.

Temporal distribution of births

The numbers of pups in individual age-dependent stages for whelping patches A and B are shown in Table 3. As both patches merged together at the time of the photographic survey, and the pupping appeared to be relatively synchronized in both patches, the data from both patches were pooled.

Figure 3A shows the fit of the model to the proportions observed from the staging survey of Patch A/B. The estimated peak of the birth distribution (the newborn/yellow stage) was on 20 March. Figure 3B shows the estimated proportion of harp pups visible on the ice as a function of time. The estimated proportion of pups on the ice was 0.99 (s.e. = 0.0001) when the photographic surveys were conducted on 28 March.

In order to explore the effect of pooling the staging data from patch A and B we fitted the staging data to patch A and B separately. The estimated proportion of pups on the ice was then 0.98 (s.e. = 0.0003) for patch A and 0.99 (s.e. = 0.0001) for patch B around noon on 28 March.

Photographic surveys

On 28 March, the area between 70°43'N 18°31'–18°15' W and 72° 01'N 17°29'–17°29'W (in practical terms, the merged patches A and B) was photographed using both aircraft simultaneously (Figure 1). The photographic survey covered all recorded whelping of harp seals. A total of 27 transects spacing 3 nautical miles were flown, resulting in 2792 photos (Table 1). Of these, 98 photos had some degree of overlap ranging from 94 m^2 to 12 896 m^2 between photos, and the total overlap area was 0.35 km^2. The total area covered by the photographic survey was ~4569 km^2. The total area covered by the photographs was ~305 km^2, i.e. about 6.7% of the covered area. In the analysis, photos with overlap were checked to avoid double counting, and the area used in the pup abundance estimation procedure was adjusted for the degree of overlap.

Correcting for readers errors

We estimated the parameters for the linear correction model for each reader. For reader 1 the estimated slope was $\hat{b}$ (s.e. = 0.005) and for reader 2 the estimated slope was $\hat{b}$(s.e. = 0.006). In both cases the intercept term was not statistically significant on a 95% level and was thus dropped from the linear correction model.

The estimated variance contributions from these corrections were V^{meas}= 291 723.

Pup production estimate

A total of 6034 harp seal pups were counted on the 2792 photos without correcting for reading errors. From this an estimated pup production of 85 968 (s.e. = 11 805) harp seal pups without any corrections was obtained. Correcting for reading error, temporal birth distribution, and overlapping photos yielded an estimate of 89 590 (s.e. = 12 310, *CV* = 13.7%) harp seal pups.

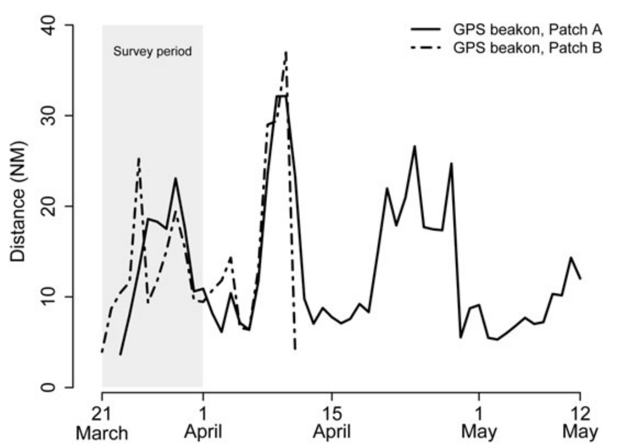

Figure 2. The daily drift ice distance observed from two satellite based GPS beacons deployed on the ice.

Stock assessment

Population modelling

The estimated population sizes and parameters used in the model, along with the normal priors used, are presented in Table 2. The modelled population trajectory with 95% *CIs* is shown in Figure 4. The dashed lines show model predictions for various catch options. Only the 95% *CI* for the model predictions of one of the catch options is shown. The widths of the 95% *CI* for the other catch options are identical, but the angle is shifted relative to the various future predictions. The model estimates were stable

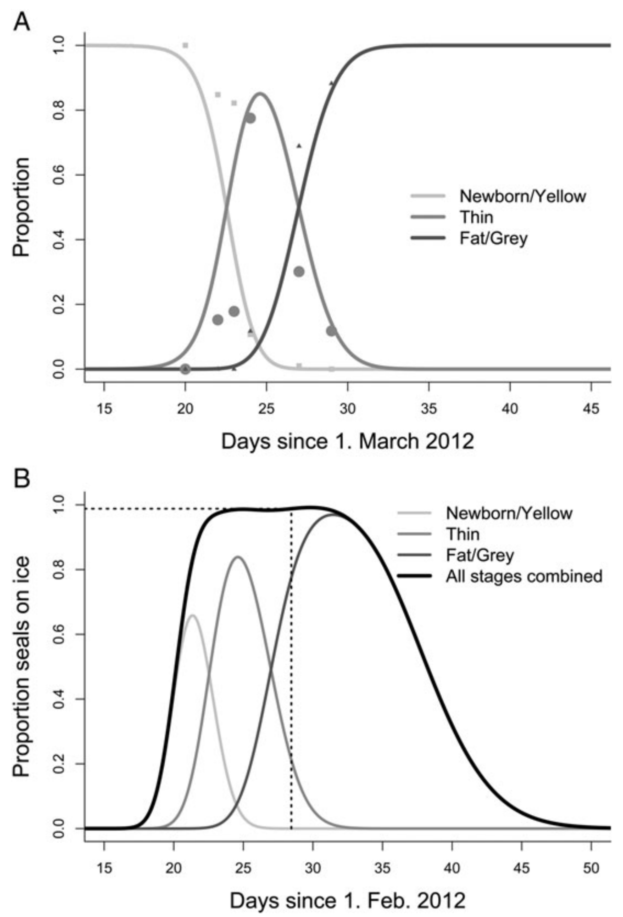

Figure 3. (**A**) Observed proportions and estimates of the probability of a harp seal pup being classified as belonging to the various stages, and (**B**) predicted proportion of harp seal pups on ice as a function of time. The dotted vertical line shows the proportion of pups visible on ice 28 March (when the photographic survey was carried out).

Table 3. Number of harp seal pups in individual age-dependent stages in the Greenland Sea during March 2012.

Date	Patch	Stages							Total
		Newborn	Yellow	Thin white	Fat white	Grey coat	Ragged jacket	Beater	
March 20	A	37	64	0	0	0	0	0	101
March 23	A	53	159	46	0	0	0	0	258
March 27	A	0	0	11	32	2	0	0	45
March 22	B	151	634	141	0	0	0	0	926
March 24	B	10	86	694	103	2	0	0	895
March 27	B	0	12	348	706	81	2	0	1149
March 29	B	0	0	79	366	225	3	0	673

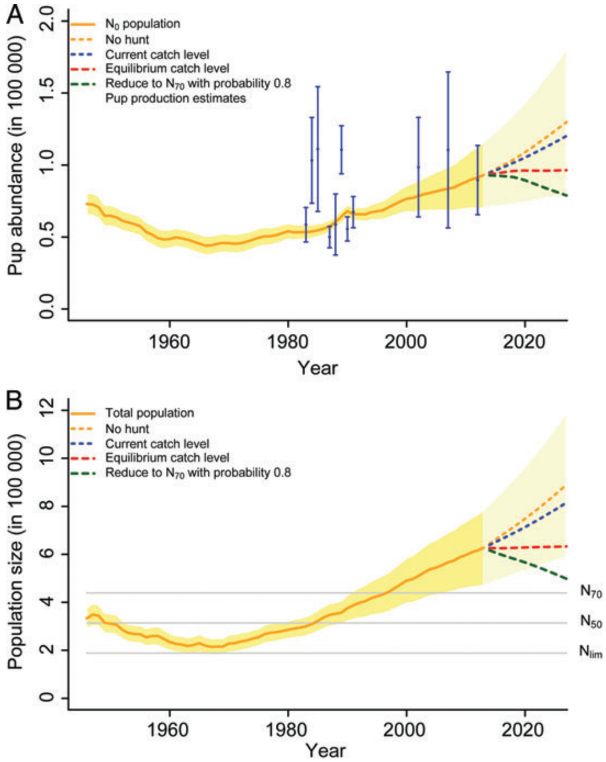

Figure 4. (**A**) Modelled pup abundance (full yellow line) with pup production estimates (blue dots with 95% *CIs*), and (**B**) modelled total population (full yellow line). Shaded areas denote 95% *CIs*, and model predictions for various catch scenarios are shown with dashed lines. The following catch scenarios were explored: no hunt (yellow), current catch level (5941, 59.9% pups, blue), equilibrium catch level (20 429, 59.9% pups, red), and reducing the population size to N_{70} with probability 0.8 (30 988, 59.9% pups, green). N_{70}, N_{50}, and N_{lim} denote 70, 50 and 30% of the historical maximum population size, respectively.

for various choices of initial values. Even though the priors for M_0, and M_{1+} are relatively non-informative, increasing the mean of the prior to 0.3 and 0.1, respectively, caused a 2% change in the total population estimate. The fit to the pup production survey data is good, in the sense that the model fit within the *CIs* of most survey estimates. The model trajectory indicates a decrease in the population size from 1946 to the 1970s, and a substantial increase in the population abundance from the 1970s till now. The model estimated a 2013 abundance of 534 400 (95% CI = 379 200–689 600) 1+ seals and 93 010 (95% CI = 70 210–115 810) pups. The total 2013 estimate was 627 410 (95% CI = 470 540–784 280) harp seals in the Greenland Sea.

Exploring various catch options

The model indicates an increase in the 1+ population of 28.8% over the next 10 years under the scenario of no hunt. If the current catch level of 5941 seals (59.9% pups) is continued, the model predictions indicates an increase in the 1+ population of 21% over the next 10 years. The model estimates that an annual catch level of 20 429 seals (assuming 59.9% pups) would stabilize the population size at the present level. The current total population size is the largest population size observed, and is thus used as N_{max} in the management regime. If the annual catch level was 30 988 seals (assuming 59.9% pups) the population would be reduced to N_{70} with a probability of 0.8 within 10 years. The trajectories of the model predictions using the various catch options are found in Figure 4.

Discussion

Previous (1977–1991) mark–recapture experiments (Øien and Øritsland, 1995) and aerial pup production surveys performed in 1991 (Øien and Øritsland, 1995), 2002 (Haug *et al.*, 2006), and 2007 (Øigård *et al.*, 2010) suggested a prevailing increase in Greenland Sea harp seal pup production. The 2012 estimate, corrected for reader error, temporal birth distribution and overlapping photos, was 89 590 (s.e. = 12 310, CV = 13.7%). Although the 2012 point estimate was lower than the estimates in 2002 and 2007, it was not significantly different from those estimates on a 5% level. This may present an indication that the pup production has not changed much over the last decade.

As in previous surveys, extensive reconnaissance surveys were conducted in the period 18 March to 1 April 2012 in all areas historically used by harp seals in the Greenland Sea (areas between 67°N and 74° N, see Øritsland and Øien, 1995; Haug *et al.*, 2006; Øigård, *et al.*, 2010). There is good evidence to conclude that previous ice conditions in the central Greenland Sea were significantly different from those observed in recent decades (Divine and Dick, 2006). These differences manifest themselves as a reduction in extent and concentration of drift ice, particularly within the region around and north of the Jan Mayen Island where the drifting ice traditionally formed an ice-peninsula (Wilkinson and Wadhams, 2005), which used to be the main harp seal breeding location (Sergeant, 1991). Observed ice reductions may have changed the seal-breeding habitat in the Greenland Sea. Could these changes in ice-conditions have triggered behavioural changes to such an extent that the seals have relocated breeding to areas outside those historically known? If so, some whelping areas may have been uncovered by the latest surveys. The consequence would be lower pup production estimates and subsequent underestimation of the actual size the Greenland Sea harp seal stock. In the 2007 breeding season one harp seal whelping patch was observed on the ice in the southernmost parts of Greenland (starting on the southeast side and then drifting around the southern tip of Greenland and northward on the southwestern side; Rosing-Asvid, 2008; ICES, 2011). Although results from genetic studies are still not available, the timing of the whelping may indicate that those on the South Greenland patch were most likely harp seals belonging to the Greenland Sea stock. This could be an indication that parts of the harp seal population have relocated their breeding areas to areas outside those historically used by the species.

The survey methods used are under continuous evaluation and development. Use of satellite images for detection of new whelping areas is being considered, and the use of drones to replace the fixed-wing aircraft for the photographic surveys is a topic for future research. Also, the task of inspecting the aerial photos is highly demanding and requires a lot of resources. Another topic for future research is development of an automatic classification procedure for this purpose.

Assuming that the estimates of the mean and s.d. of pup stage length were as given by Kovacs and Lavigne (1985), results from the pup staging operations showed that the majority of harp seal females in the Greenland Sea whelped between 19 and 24 March in 2012. This is almost identical to the situations observed in 2002 (Haug *et al.*, 2006) and 2007 (Øigård *et al.*, 2010), and is in accordance with observations made in the area in 1991, whereas in 1990 the breeding may have peaked 5–7 days later (Øritsland and Øien, 1995).

In both 2002 and 2007, small harp seal whelping patches were detected immediately south of the main patches during 3–5 April (see Haug *et al.*, 2006; Øigård *et al.*, 2010). To assess whether this might also be the case in 2012, extensive aerial surveys were conducted south of the main patch on 1 April, but no pups or breeding seals were observed.

In estimating the total population size, we used an age-structured population model developed and accepted for use in ICES assessments of harp seals both in the Greenland Sea and in the Barents Sea/White Sea (ICES, 2011). Field data on the age distribution of the Greenland Sea harp seal population is not available, so the model has to assume that the age structure in the catch data represents the age structure of the population. In reality the age structure of the catch data are biased for several reasons (see also Kjellqwist *et al.*, 1995): the preferences among hunters have changed over the decades (in some cases adult males were preferred), younger seals may be easier targets than older seals, and there is obviously a sex- and age-based segregation of harp seals on the moulting grounds where the hunt for adult seals occurs. Potential changes in reproductive parameters have not been taken into account when evaluating the model predictions under the various catch scenarios. The catch data does not provide information about the sex ratio in the catches, only the total catches distributed over pups and 1 + animals. The population model estimates total abundance, but assumes that 50% are females contributing to the production (based on data on reproduction). If a higher proportion of females than males was caught, the model estimates would be positively biased.

Whereas the Greenland Sea stock of harp seals have been subject to commercial exploitation for centuries, the hunting pressure has been substantially reduced during the past three to four decades (Iversen, 1927; Rasmussen, 1957; Nakken, 1988; Sergeant, 1991; Haug *et al.*, 2006; ICES, 2011). Based on cpue analyses and mark–recapture pup production estimates, it has been assumed that the population may have increased since the early 1960s, although direct evidence has been limited (Ulltang and Øien, 1988; Øien and Øritsland, 1995). The current population model runs confirm that the population may have increased in size since around 1970, and yield an estimated 2013 total abundance of ca. 627 400 harp seals. Even though it has been predicted that the population could continue to increase under the current harvest regime of very small annual removals, the lack of trend in pup production may indicate a population approaching its current carrying capacity (K). Despite stabilization of pup production, the total population may continue to increase for some time as a result of recent reductions in female fertility in the population (ICES, 2011). The mark–recapture estimates of pup production from 1983–1991 appear to have a strong influence on the modelled pup abundance. Those estimates are somewhat indecisive as they vary substantially between years. Fluctuations on this scale are hardly natural, but rather a sampling artefact (see Øien and Øritsland, 1995). Hence the uncertainty may have been underestimated. Nevertheless, the lowest estimates have the smallest uncertainty and therefore the highest confidence in the model, and we see an increasing trend in the pup abundance with a possible stabilization after 2000. Although it may seem premature to conclude that the pup production has stabilized, it is no doubt a plausible possibility. Another survey in 3–5 years is needed to shed further light on this. However, if the population is approaching K, one should definitely consider adding density dependence to the population model in the future. The current model predictions do not take into account any density dependence, and if the population is near K they are positively biased, which again makes the estimated catch levels positively biased. It is important to notice, however, that the annual fecundity rates in harp seals can be highly variable. In the Northwest Atlantic, where annual estimates of fertility are available for the harp seal population over a period spanning from 1954 to the present, the proportion of pregnant females has been observed to vary from 40% to >85% from year to year (ICES, 2011). Such changes may certainly account for rapid changes in pup production, which are not necessarily an indication of a sudden population decrease or increase. Recent (2009) mean age at sexual maturity in Greenland Sea harp seal females was observed to be significantly higher than the long-term (1964–1990) average, and current fertility of mature females is observed to be lower than it was two to three decades ago (ICES, 2011).

The estimated population growth of Greenland Sea harp seals over the past four decades is comparable with the development in the Northwest Atlantic population of the species (see Hammill and Stenson, 2010). However, while the Greenland Sea population has increased from a mid 1970s size of ~35% of the current level, the Northwest Atlantic population size in the mid 1970s was only 22% of the current level (8.2 million individuals). Why the Greenland Sea population exhibits slower growth than the Northwest Atlantic population is unknown. It is worth noticing that Barents Sea/White Sea harp seals, the other Northeast Atlantic population, has faced even more severe problems. A slow increase in the population from the mid 1970s (Skaug *et al.*, 2007) to a peak during the early 2000s, was followed by a recent dramatic pup production decrease, resulting in a current level of ~1.4 million individuals (ICES, 2011).

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