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RECENT HARP AND HOODED SEAL PUP PRODUCTION ESTIMATES IN THE GREENLAND SEA SUGGEST ECOLOGY-DRIVEN DECLINES

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ABSTRACT

Pup production of the Greenland Sea populations of harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals were estimated based upon aerial surveys in March 2018. One fixed-wing aircraft was used for large-area reconnaissance flights to identify the whelping concentrations and to carry out photographic surveys along systematic transects over the whelping areas. A helicopter, operated from an ice-going vessel, flew more localised reconnaissance flights, deployed GPS beacons within the detected whelping concentrations to monitor ice movements, and determined the proportion of pups in specific age-related developmental stages. While the entire estimated pupping region should ideally be covered during one day, photographic surveys in 2018 were carried out on two consecutive days, March 27 and 28, with slightly different survey designs between the two days to account for potential gaps in coverage caused by changes in visibility and cloud cover. Surveys on the two days were partially overlapping, and pup production estimates were consistent when using different combinations of transects from the two days, suggesting that these photographic counts give a relatively robust estimate of pup production in 2018. The combination of surveys that was deemed most appropriate (in terms of maximum coverage with minimum risk of double coverage) yielded an estimated harp seal pup production of 54,181 (SE=9,236, CV=0.17), which is significantly lower than estimates obtained in similar surveys in 2002, 2007, and 2012. Estimated hooded seal pup production was 12,977 (SE=1,823, CV=0.14), which is lower than estimates obtained from surveys in 2005 and 2007, but similar to estimates from the most recent survey in 2012. The reasons for these declines are unknown, but similar declines in the Barents Sea and White Sea harp seals in the mid-2000s suggest that large-scale environmental or ecological changes affecting the Barents Sea and the Norwegian Sea may be important factors.

Keywords: Harp seals, hooded seals, pup production, population assessment, population modelling, aerial survey, strip transect, Arctic

INTRODUCTION

Estimating abundance and monitoring changes in population size are critical for the management of harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals. Such information is also important for assessing potential ecosystem responses to environmental variability. Both species have been harvested for centuries in the North Atlantic (Sergeant, 1991; Stenson, Haug, & Hammill, 2020; Stenson, Myers, Ni, & Warren, 1997; Øigård, Haug, & Nilssen, 2014a, 2014b), and one of the primary goals of the regular population assessments is to provide advice on the harvest potential of each species. Using catch-at-age data, sequential population models and mark-recapture data to estimate population abundance of animals in the wild are associated with several underlying assumptions, each with substantial uncertainties associated with them. Independent estimates of pup production, using systematic aerial photographic or visual strip transect methods, have therefore been recommended and used since the mid-1980s to provide the basis for estimates of total abundance of harp and hooded seals in the Northwest Atlantic (Bowen, Myers, & Hay, 1987; Hammill, Stenson, & Myers, 1992; Stenson et al., 1993, 2002; Stenson, Hammill, & Lawson, 2010; Stenson, Hammill, Lawson, & Gosselin, 2006; Stenson, Hammill, Lawson, Gosselin, & Haug; Stenson, Hammill, Lawson, Gosselin, & Haug, 2005; Stenson et al., 1997; Stenson, Rivest, Hammill, Gosselin, & Sjare, 2003), Greenland Sea (Haug, Stenson, Corkeron, & Nilssen, 2006; ICES, 2006b; Salberg, Haug, & Nilssen, 2008; Øigård et al., 2014a, 2014b; Øigård, Haug, Nilssen, & Salberg, 2010; Øritsland & Øien, 1995) and White Sea (ICES, 2019; Potelov, Golikov, & Bondarev, 2003). Total population sizes and status of the stocks are subsequently estimated by fitting age-structured population models, which incorporate annual reproductive rates and removals, to the independent estimates of pup production (e.g., Hammill & Stenson, 2007; Healey & Stenson, 2000; ICES, 2019; Skaug, Frimannslund, & Øien, 2007; Øigård et al., 2014a, 2014b).

Harp and hooded seal pup production were last assessed in the Greenland Sea in 2012 (Øigård et al., 2014a, 2014b). The accepted management approach for these populations (ICES, 2006a) requires that there is a time series of at least three pup production estimates spanning a period of 10–15 years where the last survey should not be more than 5 years old. If surveys and/or associated data are more than 8 years old, the population does not meet the 'Data Rich' criteria and the

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harvest advice that can be provided is limited and should be more precautionary (ICES, 2006b). To meet these ICES criteria, new surveys to obtain data necessary for estimation of the abundance of the Greenland Sea harp and hooded seal stocks were conducted in 2018. These pup production estimates represent one key input into a deterministic population dynamics model used for estimating past and present total population size, and to estimate future population trajectories under various hunting quota regimes (Øigård et al., 2014b).

During the period 1977–1991, about 17,000 harp seal pups were tagged in a comprehensive mark-recapture experiment in the Greenland Sea (Øien & Øritsland, 1995). Pup production estimates based on this experiment varied by almost a factor of 2 between consecutive years, from around 60,000 in 1983, 1987, 1988, 1990 and 1991, to over 100,000 in 1984, 1985 and 1989 (ICES, 2001; Ulltang & Øien, 1988; Øritsland & Øien, 1995). The first aerial survey was carried out in 1991, resulting in an estimate of pup production (55,300, SE=7,800) that was relatively similar to the estimate obtained from a mark-recapture experiment the same year (67,300, SE=5,500, ICES, 2001). Following an 11-year gap, aerial surveys have been carried out at roughly 5-year intervals, starting in 2002 (Haug et al., 2006) when harp seal pup production was estimated to be 98,500 (SE=16,800), i.e., similar to the higher estimates from the 1980s. The 2007 survey yielded an even higher pup production estimate (110,530, SE=27,680; Øigård et al., 2010) but the 2012 survey estimate was again lower, at 89,590 (SE=12,310, Øigård et al., 2014b). Unfortunately, no conclusions can be drawn about whether any changes in pup production have occurred since the early 2000s due to the wide confidence limits associated with these last three survey estimates (Øigård et al., 2014b).

While the primary objective of the 2018 surveys in the Greenland Sea was to estimate the pup production of harp seals, a second objective was to obtain a new pup production estimate for hooded seals. While the two species previously required separate surveys, their breeding patches have now become more overlapping, facilitating the simultaneous assessment of both species. This is most likely a result of the westward contraction of the pack ice belt towards the Greenland coast (Stenson et al., 2020). Previous aerial surveys of Greenland Sea hooded seals conducted in 1997 (ICES, 1999), 2005 (Salberg et al., 2008), 2007 (Øigård et al., 2010) and 2012 (Øigård et al., 2014a) suggested a decline from ~24,000 in 1997 to around 14,000–16,000 during the later surveys. The 1997 pup production was a minimum estimate, as it was not corrected for the temporal distribution of births or pups born outside of the whelping patches (ICES, 1998). In contrast, the 2005 and 2007 estimates both corrected for temporal distribution of births as well as potential reader bias, while the 2012 estimate was also corrected for overlapping photos. All estimates since 2005 were similar (Øigård et al., 2014a). Hooded seals have been protected in the Greenland Sea since 2007 (ICES, 2006b, 2019). The 2012 estimated pup production was similar to previous surveys but this could be expected given that catches are almost exclusively young of the year and hooded seals reach sexual maturity at 4–5 years of age (see Frie, Stenson, & Haug, 2012). Because the pup production in 2007 and 2008 was so small, any impact of protection may not have been visible when these cohorts first entered the breeding population (at around age 4–5). However, the additional 6-year period until the 2018 survey should have allowed the breeding population to increase gradually, resulting in a detectable change in pup production by this time.

The 2018 Greenland Sea seal survey was carried out with the aims to meet the ICES management objective for maintaining the harp and hooded seal populations as data rich, and to monitor the continuing trend in hooded seal pup production following a 10-year pause in hunting. While harp seals were the main focus, given the need to update hunting quotas, previous surveys have shown that hooded seal whelping patches are generally overlapping spatially with harp seal patches, allowing both species to be effectively surveyed simultaneously.

MATERIALS & METHODS

Logistics

The survey used a combination of ship-based, helicopter and fixed-wing aircraft operations covering the period March 15 to 30. An ice-strengthened coastguard vessel (MS Svalbard) was used for operations in the Greenland Sea drift ice. The ship was equipped with a helicopter platform and equipment in compliance with relevant requirements for helicopter operations. An Ecureuil AS 350 B1 helicopter was used to conduct reconnaissance flights, to monitor the distribution of seal patches and to perform age-staging of pups. A fixed-wing Twin Otter aircraft (TF-POF) was used to conduct reconnaissance and photographic surveys. The aircraft was based at Akureyri (Iceland) and at Nerlerit Inaat airport (Constable Pynt, 50 km north of Scoresby Sound, East Greenland).

Reconnaissance surveys

Reconnaissance surveys were carried out by the fixed-wing and helicopter from March 18 to 30. The ice cover in 2018 was considerably reduced compared to previous surveys in 2007 (Øigård et al., 2010) and 2012 (Øigård et al., 2014a, 2014b), with the edge of the pack ice located closer to the East Greenland coast. Nevertheless, most of the ice itself still appeared to be of sufficient quality and, therefore, suitable for pupping and nursing. In addition to examining the general areas of suitable ice near the latitudes historically used for pupping by harp and hooded seals in the Greenland Sea (Haug et al., 2006; Salberg et al., 2008; Øigård et al., 2014a, 2014b; Øigård et al., 2010), reconnaissance flights also covered areas to the north and south of these historical core areas to account for potential distributional changes (see results). Figure 7 in Stenson et al. (2020) provides a general sense of the distributional overlap of all historical surveys, and indicates a general southward shift in distribution of pupping areas between the 1990s and 2000s. Since fixed-wing operations are based at airports in either Iceland or the Scoresby Sound area in Greenland, reconnaissance carried out during transits also cover areas far to the south of the main pupping areas. Any pupping patches in these areas would therefore have been discovered and, thus, also covered by the photographic surveys. As for pack ice regions towards the north, reconnaissance surveys have been flown up to and beyond 75°N in all previous surveys, without any signs of breeding aggregations. Given the general southward shift in the main breeding patches since 2000, the probability of major new breeding patches having been established even further north is almost certainly very small. This is also supported by the lack of observations of breeding harp or hooded seals from pack ice areas around Svalbard (personal communication, Norwegian Polar Institute). Helicopter reconnaissance flights were usually flown as parallel east/west transects at a spacing of ~5 nm and an altitude of 160–300 m. Transects were adapted to the ice conditions encountered during the survey period, with the ice edge generally delineating the eastern end and areas of fast ice along the Greenland coast making up the western end. Due to the significant southward ice drift that occurs in the region caused by the East Greenland Current, and a pupping period that often spans several weeks (Øigård et al., 2014b), most areas were surveyed repeatedly to minimise the risk of missing whelping concentrations. Colour dye markers and 5 satellite-based GPS beacons were deployed in, and around, the major whelping concentrations to facilitate relocation and to monitor ice drift throughout the survey period.

The Twin Otter aircraft was used to search for potential seal whelping areas within the drift ice outside of the historical core area, these reconnaissance flights were usually flown at an altitude of 300 m (range 200–330 m), and followed east-west transects usually spaced 10 nm apart, although spacing was decreased to 5 nm in areas where seals were observed.

Pup staging surveys

To correct the estimates of abundance for seal pups that had left the ice or were not yet born at the time of the survey, it was necessary to estimate the temporal distribution of births throughout the pupping season. This was done by using information on the proportion of pups in distinct age-dependent stages. These easily recognisable descriptive age categories were based on pelage colour and body condition, overall appearance, and muscular coordination, as described for the Northwest Atlantic harp and hooded seals by Bowen et al. (1987), Stenson & Myers (1988) and Stewart & Lavigne (1980), and subsequently used in surveys in the Greenland Sea (Salberg et al., 2008; Øigård et al., 2010, 2014a, 2014b).

Normally, pup staging surveys are carried out at least three times throughout the pupping season. Due to a combination of inclement weather and the early departure of the vessel from the breeding area (March 23), only one pup staging survey was carried out in 2018, on March 21.

Photographic surveys

Photographic surveys were carried out on March 27 and 28. The Twin Otter was equipped with a digital camera (Phase One IXU-RS-1000/Lens: Rodenstock 50 mm f/4.0). Images were taken at an altitude that was maintained at 1,100 ft (335 m) using a radar altimeter, and at a flight speed of approximately 130 knots. The camera was operated to cover 80–90% of the area along each transect line, with deliberate spacing between adjacent images to avoid overlap and the potential for double counting. The image footprint was 347 m (cross track) x 260 m (flight direction), with a pixel ground resolution of approximately 29 mm. Transects were flown along east-west lines at a latitudinal spacing of 1–3 nm.

During previous surveys, the ship and helicopter were used in addition to GPS beacons deployed on the ice to define the geographic range of the whelping patches prior to the fixed-wing aircraft photographic survey. Since the ship and helicopter were forced to depart from the ice prior to the optimal time for the photographic surveys in 2018, the last helicopter reconnaissance flight was carried out on March 22. For the remainder of the reconnaissance flights conducted until March 30, the aircraft was guided to the whelping patches based only on the GPS beacons. Cameras were turned on when seals were observed on a transect line. Cameras were turned off when the transect line ended at the eastern ice edge, or when no seals were observed for a 15-minute period while continuing the transect line towards fast ice in the west, or when fast ice had been encountered.

Photographic counts

All photos were orthorectified to Universal Transverse Mercator projection (UTM, zone 32N). They were analysed by two experienced readers, using custom-made routines in the QGIS GIS package (QGIS Development Team, 2016). After reading all photographs, the readers re-read a series of their photographs in sequence to determine if identifications had improved over the course of the readings. Photos were read until the second readings were consistently within 1% of the first. The original readings were replaced with the second readings up to this point. A random subset of ~100 photos were re-read to ensure that the first and second readings were consistent.

To correct for misidentified pups, a subset of photos was selected and read by both readers. Initial comparison of these readings revealed a relatively consistent difference between the readers, with one reader consistently overlooking seals that were identified by the other reader (and confirmed by a third independent reader). To obtain a corrected estimate for this reader, we fitted a linear model of the form:

$$n_{j,k}^{r1} = \alpha + \beta n_{j,k}^{r2} + \epsilon_{j,k}$$

where $n_{j,k}^{r1}$ is the counts by the more precise reader for the k^{th} photograph in the jth transect, $n_{j,k}^{r2}$ is the counts to be corrected from the other reader, α is the estimated intercept, β is the estimated slope, and $\epsilon_{j,k}$ represents a residual error term assumed to be normally distributed with zero mean and standard deviation. Using the estimated parameters we applied a linear correction model for each of the original counts:

$$\hat{n}_{j,k}^{r2} = \alpha + \beta n_{j,k}^{r2}$$

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

$$\epsilon_{j,k} = \sigma^2 + var(\alpha) + 2cov(\alpha,\beta) n_{j,k}^{r2} + var(\beta)(n_{j,k}^{r2})^2$$

where $var(\alpha)$ is the variance of the intercept, $var(\beta)$ is the variance of the slope, and $cov(\alpha,\beta)$ is the covariance between the intercept and the slope.

Pup production estimation

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):

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

where $W_j = l_j / A_j$, A_j is the area covered of all photographs on transect j, l_j is the length of transect j, J is the total number of transects, and $x_j = \sum_{k=1}^{P_{ij}} \hat{n}_{j,k}$ 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 the survey. This estimator takes into account changes in transect width along transects and between transects due to changes in flight altitude. The estimates of error variance V^s, based on serial differences between transects were calculated as (Salberg et al., 2008):

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

This estimator assumes that the mean is constant between two neighbouring transects. For the seal pup data this assumption is often not valid due to clustered data, and we will have an unwanted contribution from the difference between the transect count mean values which causes an overestimate of the variance of the pup production estimate (Cochran, 1977). However, if the seals are homogenously spread over a large area this assumption is fine.

The variance associated with misclassification of pups, i.e., readers errors, for the whole survey is then (Salberg et al., 2008):

$$V^{meas} = T^2[\sum_{j=1}^{J} W_j^2 \, P_j \sigma^2 + (\sum_{j=1}^{J} W_j \, P_j)^2 var(\alpha) + 2cov(\alpha,\beta)(\sum_{j=1}^{J} W_j \, P_j)(\sum_{j=1}^{J} W \, j \sum_{k=1}^{P_j} n_{j,k}) + var(\beta)(\sum_{j=1}^{J} W \, j \sum_{k=1}^{P_j} n_{j,k})^2]$$

If the intercept term is not statistically significant on a specified level it could be dropped from the linear correction model. The variance expression is then simplified to:

$$V^{meas} = T^2[\sum_{j=1}^{J} W_j^2 \, P_j \sigma^2 + (\sum_{j=1}^{J} W_j \, P_j)^2]$$

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.:

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

Pup visibility to aerial surveys

Temporal distribution of births and predicted proportion of pups present during photographic surveys

As described previously in Øigard et al. (2010), the temporal distribution of births for both harp and hooded seals was estimated using the method developed in Reed & Ashford (1968) and adapted for modelling the birth distribution for harp and hooded seals in Bowen et al. (1987), and Myers & Bowen (1989). The life cycles of the seals were assumed to be divided into k identifiable age-dependent stages $S_1, \ldots, S_k$. Birth takes place into stage S_1 and the pup then progresses in succession through stages $S_1, S_2, \ldots$ until it attains maturity when reaching stage S_k. All pups reaching stage S_k eventually die in that stage, either from hunting or natural causes (Reed & Ashford, 1968). We assumed that for both seal populations the birth rate could be adequately described by a continuous function of time, $m_1(t)$ which denoted the temporal distribution of births. The distribution of births over time was assumed to be a normal distribution with mean value μ_1 and standard deviation σ_1.

The various development stages are denoted by the subscript j, and a pup passes from stage j to stage $j+1$. The stage durations are specified in terms of transition intensity functions $\phi_j(t)$, which is the probability that an animal passes from stage j to $j+1$ in the interval $[\tau, \tau + \Delta t]$ and has survived. Here τ is the time spent in stage j. The stage duration was assumed to be a semi-Markov process, i.e., the transition intensities depend only on the current stage and the time so far spent in that stage (Bowen, Myers, & Hay, 1987). The rate at which pups enter the stage j at time t were denoted by $m_j(t)$ and given by a recurrence relationship Myers & Bowen (1989):

$$m_j(t) = \int_0^\infty m_{j-1} \, (t-\tau)\phi_{j-1}(\tau) d\tau \quad j = 1, .., k$$

The proportion of pups that will be observed on the ice in stage j at time t is (Bowen, Myers, & Hay, 1987; Myers & Bowen, 1989):

$$n_j(t) = \int_0^\infty m_{j-1} \, (t-\tau)(1 - \int_0^\tau \phi \, (s) ds) d\tau$$

This equation assumes no pup mortality during these stages and that all pups on the ice are visible. In Bowen et al. (1987), Bowen, McMillan, & Blanchard (2007) and Myers & Bowen (1989) the transition intensity functions $\phi_j(t)$ were assumed to follow a Gamma distribution with shape parameter κ_j and scale parameter ρ_j for stage j. The product between the shape parameter and the scale parameter, $\rho_j \kappa_j$, gives the mean duration of stage j. The numbers of individuals observed to be of stage j at time t_i were denoted S_{ij}. The S_{ij}'s were obtained by taking a random sample of the pup abundance and determining the stage of each individual. The predicted proportions of each stage present at time t_i, P_{ij}, are calculated as in Myers & Bowen (1989), i.e., by estimating the parameters $\hat{\mu}_1$ and $\hat{\sigma}_1$ of the birth distribution. The proportion of pups on the ice at time t was estimated using (Salberg et al., 2008; Øigård et al., 2010):

$$Q(t) = \sum_{j=1}^{k} \eta_j \, (t)$$

The estimated variance of the proportion of pups on the ice at a given time was estimated by simulating from the proportion of pups in the various stages obtained from the staging by simulating from a multinomial distribution with k stages (Salberg et al., 2008).

Ideally, at least three staging surveys should be carried out in order to obtain robust estimates of the temporal distribution of births and the proportion of pups in different developmental stages. However, due to a combination of the premature departure of the survey vessel from the ice, and poor weather conditions during the last few days prior to departure, estimates of the proportion of harp and hooded seal pups in each developmental stage were only obtained for March 21. To partially compensate for the lack of staging data, we also attempted to stage pups in a crude way based on the aerial images obtained (see details below). To obtain an estimate of proportion of seals on ice at the time of the photographic surveys, we used the fitted curves from the 2012 survey (see below).

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:

$$\hat{N}^{corr} = \frac{\hat{N}}{\hat{Q}}$$

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

The estimates of N_i 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 (e.g., Casella & Berger, 1990):

$$V^{corr} = (\frac{1}{Q})^2 V(\frac{N}{Q^2})V^q$$

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

Estimating stage progression in 2018

To make up for the lack of staging surveys in 2018, we used the predicted proportions of pups in each stage for each day in 2012. We assumed that, while the absolute timing of the entire 2018 pupping season may be shifted relative to the 2012 survey, the duration of the different stages, and therefore the relative proportions of pups in each of these for every day, followed the same progression over time. By comparing the proportion of pups within each stage observed during the staging surveys on March 21 in 2018, to the predictions from the 2012 staging model fits, we obtained an estimate of the day in 2012 on which the absolute difference in proportions was at its minimum, i.e.:

$$t^{corr} = \min_t(\sum_{j=1}^{k} |\,\eta_j^{obs} - \eta_j^{pred}(t)|) \quad \{0 < t < \infty\}$$

where η_j^{obs} is the observed proportion in stage j on March 21, and $\eta_j^{pred}(t)$ is the vector of predicted proportions in stage j over time. Based on the time difference between t^{corr} and the true survey date (i.e., March 21), we could determine an optimum time correction by which to shift survey timing in 2018 (staging as well as photographic surveys) to equivalent dates, had the 2018 surveys been carried out in 2012. This allowed us to determine the best correction factor, $\hat{Q}$, for proportion of seals on ice during photo surveys.

RESULTS

Identification of whelping areas

The vessel encountered the ice edge at 72°30′N/17°55′W on March 17. Helicopter reconnaissance flights were flown from the ship between March 18 and 22, following transects varying in length from 10–30 nm in areas between 71°25′N and 73°40′N (Figure 1). The fixed-wing aircraft conducted reconnaissance flights between March 18 and 31, covering extended areas north (to 74°47′N/13°58′W) and south (to 68°40′N/24°50′W) of those covered by helicopter (Figure 1). In the north, fixed-wing reconnaissance was flown more in relation to ice distribution (also covering some areas of partial ice cover or even open water), and was occasionally restricted due to fog banks covering parts of the area. In total, reconnaissance surveys covered an area of approximately 64,000 km².

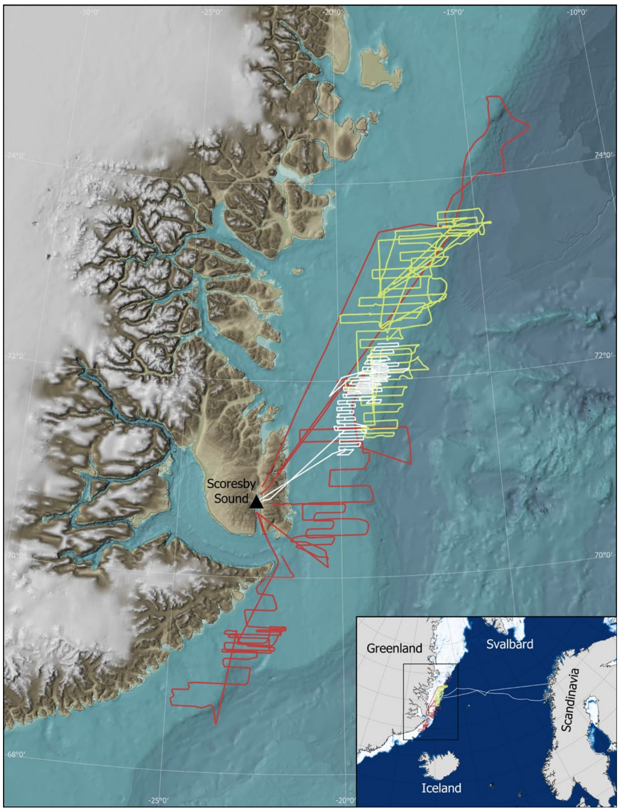

Figure 1. Reconnaissance surveys conducted by the fixed-wing aircraft (red) and helicopter (yellow) in the Greenland Sea during the period 18–30 March 2018. Also shown are the final photo surveys (white). The white line in the inset map represents the ship's track between Norway and the Greenland Sea.

On March 18, the fixed-wing aircraft located a mixed whelping patch containing an estimated 300 harp and hooded seals at approximately 74°00′N/13°47′W. No harp seals were observed during fixed-wing surveys in the southmost parts of the entire reconnaissance area, although scattered hooded seal families (defined as adult female and pup, accompanied by an adult male) were observed. An area with more concentrated hooded seal families was observed from the helicopter between 71°25′N and 71°33′N, and a GPS beacon (numbered in advance but not released sequentially) was deployed in position 71°30′N/19°06′W (Beacon 2, Figure 2) to follow the drift of this potentially emerging patch. However, no seal aggregations were found during subsequent reconnaissance flights with the fixed-wing around the southward moving position of this beacon. It is possible that poor weather conditions during the days following the deployment of this beacon may have disintegrated the ice in this region, thus also disrupting the formation of a breeding patch. It is therefore possible that some hooded seals were missed during the final aerial photo surveys, and that the hooded seal pup production is slightly underestimated.

During helicopter reconnaissance flights on 21 March a large patch of whelping harp and hooded seals was located between 72°25′N and 73°35′N; 14°30′W and 16°00′W with more possibly to the south. Colour markers and GPS beacons were deployed on ice floes at this assumed northern (73°32′N/15°43′W) and eastern (73°27′N/14°56′W) edges (Beacons 5 and 1 respectively, see Figure 2). The eastern beacon was deployed in more loose ice where breeding harp seals were observed on strips of suitable ice. Subsequent helicopter staging flights in the patch confirmed that breeding seals were distributed more toward the south than initially assumed, and another GPS beacon was deployed in position 73°13'N/16°33'W on 22 March (Beacon 3, Figure 2).

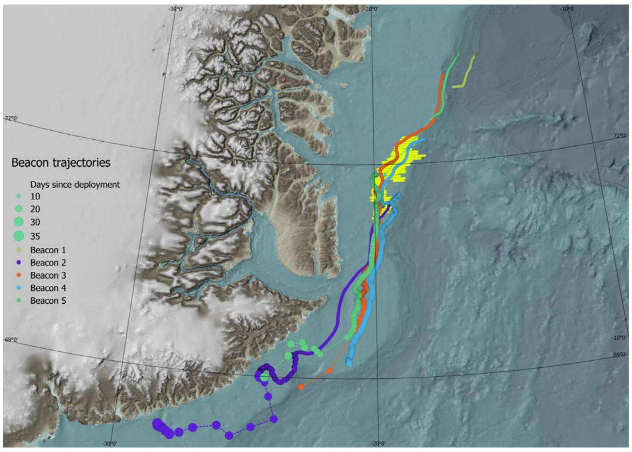

Figure 2. Trajectories of five GPS beacons deployed in the vicinity of the whelping grounds identified during helicopter and fixed wing reconnaissance surveys. Yellow lines represent transects during the aerial surveys carried out on March 27 and 28.

Due to inclement weather and visibility conditions, no helicopter operations were conducted on March 23, and instead the vessel was used to localise the north-south extent of the patch. The northern end now appeared to be around 72°52'N/16°40'W, which was close to the northernmost GPS (Beacon 1). Harp seals dominated this northern part of the patch (south to around 72°22'N/17°20'W), while hooded seals were dominant in the southern area. The remaining GPS beacon was deployed in the assumed southern end of the patch in position 72°19'N/17°39'W (Beacon 4, Figure 2), before the vessel left the area to return to Norway.

The fixed-wing aircraft continued to conduct reconnaissance surveys after the vessel departed for Norway. Based on the best estimate of whelping progression (from the one pup staging on March 21) and observations made during these surveys, and using geographic information from the GPS beacons, photographic surveys were conducted on 27 and 28 March. Subsequent reconnaissance surveys were conducted during 29–31 March to ensure that all whelping patches had been covered by the photographic surveys.

The ice drift varied substantially throughout the survey period, as seen from the GPS beacons deployed on the ice (Figure 2). Daily displacements of 15–20 nm were recorded (mean velocity: 0.21 kts, max velocity: 0.81 kts, Figure S1). The trajectories followed a generally south-southwesterly path. However, in the period 27–28 March, when the photo surveys were conducted, the wind shifted from predominantly northerly winds to south and then southwesterly winds. This was associated with very complex ice movements within the survey region, as evidenced by dramatically different ice conditions on the two days and the entirely different trajectories of the two GPS beacons that were still in the vicinity of the whelping patch (Figure 3). In general, drift of the pack ice appears to have maintained a mostly southwesterly course, while the looser pack ice along the eastern edge appeared to have been strongly affected by the SSE winds, resulting in more northeasterly drift and signs of large-scale rotational movements (Figure 3).

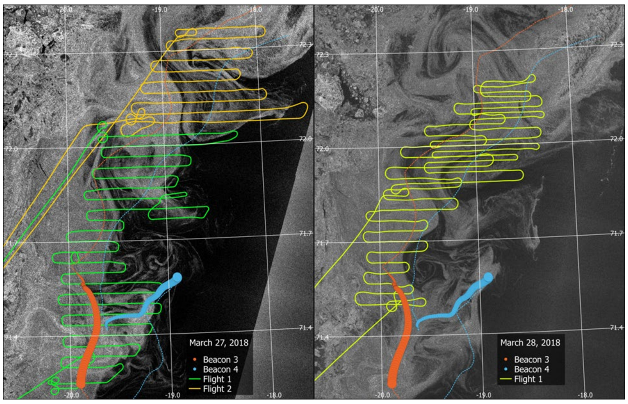

Figure 3. Aerial photo survey tracks and trajectories from two GPS beacons, overlaid on images of ice conditions on the consecutive photo survey days (March 27–28). Dashed lines represent the complete beacon trajectories, while the dots represent paths over the two survey days (dot size increases over time). Both images are from the Synthetic Aperture Radar (SAR) product, the one from March 27 was taken by the Sentinel S1A satellite at 08:11:58 UTC (March 27), and the one from March 28 by the Sentinel S1B satellite at 13:40:39 UTC, with a ground resolution of ~40 x 120 meters (X x Y). Note: Graticule labels in the figure are in decimal degrees, while coordinates in the text are in degrees and minutes.

Temporal distribution of births

Harp seals

The number of pups in individual age-dependent stages on March 21 are shown in Table 1A. To conform to the procedure used in 2012, we used the following binning of the various stages of the harp seal pups: stage 1 = Newborn/Yellow, stage 2 = Thin white, and stage 3 = Fat white/Greycoat.

Figure S2A shows the predicted proportions in different stages based on the model fitted to the 2012 data, and reported in Øigård et al. (2014b), along with the observed proportions observed during the staging survey on March 21 2018. The best fit for the observed 2018 proportions suggested that the equivalent date in 2012 would have been March 24, providing us with a time correction of 3.4 days. Applying this correction to the dates when aerial surveys were carried out in 2018 (i.e., March 27 and 28), suggested that the equivalent dates in 2012 would have been March 30 and 31. Figure S2B shows the predicted proportion of harp seal pups visible on ice as a function of time, based on the model fitted to 2012 staging data (Øigård et al., 2014b). Based on the fitted curves from 2012, and accounting for the shift in dates using the method described above, the estimated proportion of pups on ice on the dates equivalent to the aerial survey dates in 2018 were 0.99 on March 30 to 0.98 on March 31 (M=0.9858, SD=0.0025). These very small correction factors are negligible but were nevertheless applied for consistency.

Hooded seals

Table 1. A) Number of harp seal pups in individual age dependent stages in the Greenland Sea. Numbers obtained during helicopter staging surveys on March 21, 2018. B) Number of hooded seal pups in individual age dependent stages in the Greenland Sea. Numbers obtained during helicopter staging surveys on March 21, 2018, or from stagings done from aerial images taken on March 27 and 28.

A	Stages							
Date	Newborn	Yellow	Thin	Fat	Grey	Ragged	Beater	Total
March 21	11	49	521	3	0	0	0	584

B	Stages					
Date	Parturient	Newborn	Thin	Fat	Solitary	Total
March 21	0	5	258	6	4	273
March 27–28		231			444	675

observed proportions to the predicted proportions based on the 2012 survey (Øigård et al., 2014a) gave an unrealistic time correction of -4.6 days, and equivalent aerial survey dates of March 16 and 17. This would result in predicted proportions on ice during days of aerial surveys of less than 0.001. The reason why this method appears to work well for harp seals but not for hooded seals is unknown, but it may be linked to the substantially shorter lactation period for hooded seals (~4 days, Bowen, Oftedal, & Boness, 1985) than for harp seals (~2 weeks, Kovacs & Lavigne, 1985). As an alternative, we used stagings from photographs obtained during the aerial survey dates. Here, it was necessary to use a different binning of stages, due to the difficulty in distinguishing between newborn, thin and fat bluebacks. The simplest approach was to merge stages 1 and 2, thereby using the following binning: stage 1 = Newborn/Thin & Fat, stage 2 = Solitary. Using a similar approach as for harp seals, the best fitting observed proportions occurred at dates equivalent to March 28, 29 (optimum time correction: 1.06 days).

Figure S3A shows the predicted proportions in different stages based on the model fitted to the 2012 data, and reported in Øigård et al. (2014a), along with the means of the proportions observed in aerial images taken on March 27 and 28 2018. Applying the time correction to the predicted proportion of seals on ice (Figure S3B) resulted in proportions of 0.86 on March 27 and 0.8 on March 28 (M=0.8335, SD=0.0185). Since these values are similar to those used in the analyses of pup counts in 2012, we decided to use our mean proportion as correction factor, as done in 2012.

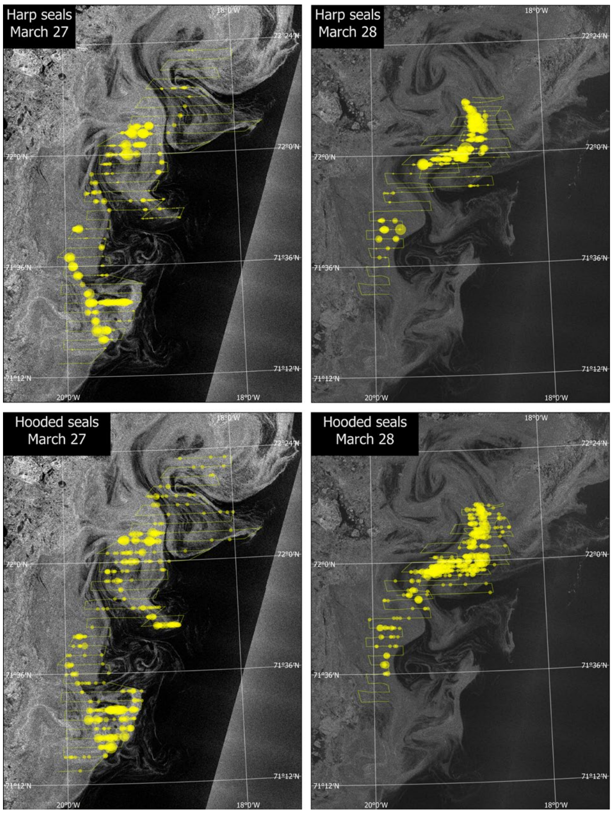

Figure 4. Photo surveys on March 27 and 28 overlaid on ice images. Each survey photography is represented by a yellow-filled circle with the radius proportional to the total number of harp and hooded seals counted on each photograph.

Photographic surveys

Two surveys with a total of 35 E/W transect lines were flown on March 27, 2018 (Figure 3 and 4; Table S1), starting at the southern end of the whelping patch at 71°15’N. The spacing between the two southernmost lines was 3 nm, while the spacing between remaining transect lines between 71°18.0’N and 72°22’N was roughly 2 nm. In total 3,005 images were taken during the two surveys on this day.

Due to fog in the northwestern parts of the area surveyed on March 27, this area was re-photographed on March 28 (Figure 3 and 4; Table S1). Based on an assessment of the ice drift (10 nm southwards over 24 hours, judged by the tracks displayed by the two satellite beacons that remained in the area), this repeat survey was conducted in an area slightly offset towards the south relative to the area that was missed during the previous day (35 transect lines, 2,088 images) between 71°30'N and 72°12'N) to ensure the same ice was covered. Transect lines were separated by 2 nm between 71°30'N and 71°52'N. Between 71°52'N and 72°12'N, where seals were most abundant, the distance between transect lines was reduced to 1 nm.

<u>**Correcting for reader 2 bias**</u>

We estimated the parameters for the linear correction models for reader 2 (see Figure S4A). The slope (β) parameters were 1.018 (SE=0.0032) for harp seals and 1.035 (SE=0.0182) for hooded seals (Figure S4B). For harp seals, the intercept term (α) was not statistically significant from zero and was therefore dropped. For hooded seals, the intercept term was significantly different from 0 (α=0.055, SE=0.0232, p=0.02). The counts for reader 2 were thus corrected for this bias using these fitted model parameters. This suggests an underestimation by reader 2 of 1.8%, and 3.5% for harp and hooded seals, respectively.

<u>**Pup production estimate**</u>

A total of 7,605 harp seal pups and 1,315 hooded seal pups were counted in the 5,093 photos from the 70 transects, without correcting for reading errors. Of these, 3,985 harps and 645 hoods were counted in the 3,005 photos from 35 transects flown on March 27, while 3,620 harps and 670 hoods were counted in 2,088 photos from 35 transects flown on March 28. The spatial distribution of seals is shown in Figure 4.

Adjusting for complex survey design

Due to the complex survey design caused by 1) flights being carried out over two consecutive days, 2) variations in transect spacing between surveys and 3) complex ice dynamics in the region during the aerial survey period (see Figure 3 and 4), we estimated pup production using various combinations of sub-surveys. The first approach was to split the data into three surveys:

1. All images from March 27; 2. All images from the northward leg on March 28; 3. All images from the southward leg on March 28.

These surveys are shown in Figure 5. The rationale for the split between northward and southward surveys on March 28 is that the transects during the initial northward leg was spaced at roughly 2 nm, while spacing between transects during the return trip towards the south was generally around 1 nm. This initial split therefore: a) separated the two survey days and b) allowed two estimates using different transect spacings (in two partly overlapping regions, see Figure 5).

Pup production estimates from these surveys for both species are presented in Table 2. For harp seals, the estimated pup production based on the March 27 survey was 51,012 (SE=10,448.2, CV=20.5%) harp seal pups and 8,227 (SE=1,364.6, CV=16.6%) hooded seal pups, prior to applying any corrections. The two partially overlapping March 28 surveys yielded combined mean estimates of 39,451 (SE=4,705, CV=11.9%) harp seals and 7,252 (SE=867.6, CV=11.9%) hooded seals. This lower estimate for March 28 is unsurprising, given the restricted latitudinal range covered compared to that covered on March 27. Direct comparison between the two is therefore not possible, and they also cannot be assumed to be completely independent. The initial strategy to use the GPS beacons to account for ice drift between the two aerial survey dates when planning transect lines for March 28 turned out to be unsatisfactory, given the very different trajectories of the two relevant beacons (Figure 3). We therefore developed a second approach to splitting the data into three different strata:

Photos from March 27 in southern region (up to 71°50.2'N) at 2 nm spacing.

Photos from March 28 (north of 71°50.2'N and up to 72°12.3'N) at 2 nm spacing. These are based on the northward leg, but extended eastwards at the same latitudes using transects 'filled in' during the southward leg (omitting overlapping stretches).

Photos from March 28, southward transect (from 72°11.6'N to 71°53'N), omitting transects at same latitudes as used in Stratum 2 in order to obtain regular spacings of roughly 2 nm. This provides an alternative estimate in a similar region.

We also created one additional fourth stratum, combined from Strata 2 and 3, with 1 nm strip distance. All these four Strata are shown in Figure 6.

Pup production estimates for these modified strata are presented in Table 3. Various combined estimates for the entire surveyed area can be obtained by combining estimates for Stratum 1 (March 27, southern region) with any either of the other 3 strata.

The mean estimates for the various combinations are relatively similar (ranging from 48,610 to 53,715 for harp seals, and from 8,976 to 9,794 for hooded seals, Table 3), although the standard error of the estimate for Stratum 4 (i.e., Strata 2 & 3 combined at half transect spacing) is substantially lower. Given the greater coverage obtained using the combination of flights on 28 March (i.e., Stratum 4), we suggest that the most robust estimate for the entire region is provided by combining Strata 1 and 4, giving estimated pup productions (prior to corrections for reader bias and temporal distribution of births) of 53,101 (SE=9,049.4, CV=17.0%) harp seal pups and 9,775 (SE=1,471.8, CV=15.1%) hooded seal pups.

It is worth noting that this is not statistically different from the estimated pup productions based on the March 27 flights only (51,012, SE=10,448.2, CV=20.5% and 8,227, SE=1,364.6, CV=16.6% for harp and hooded seal pups respectively, see Table 2).

Using Strata 1 and 4 combined, and after correcting for reader bias and temporal birth distribution, we obtained estimated pup productions of 54,181 (SE=9,236, CV=17.0%) for harp seals and 12,977 (SE=1,823, CV=15.1%) for hooded seals.

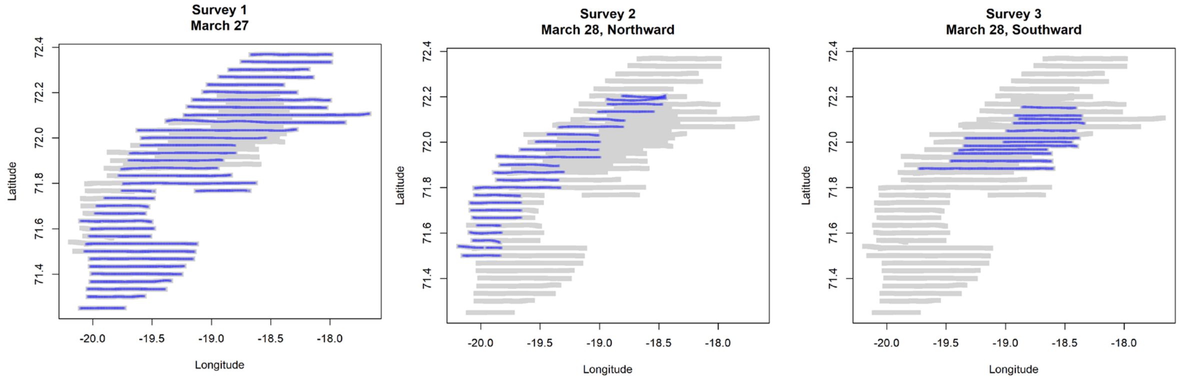

Figure 5. Maps showing the distribution of photographs designated to the three surveys (blue), overlaid on all surveys combined (grey).

Table 2. Uncorrected pup production estimates for separate surveys. Survey 1: March 27, Survey 2: March 28, northward, Survey 3: March 28 southward.

Species	Survey	Count	N	SE	lowerCI	upperCI	CV
Harp	1	3,985	51,012	10,448.2	40,564	61,460	20.5
Harp	2	1,281	17,123	3,303.8	13,819	20,427	19.3
Harp	3	2,339	22,328	3,353.6	18,974	25,682	15
Hood	1	645	8,227	1,364.6	6,862	9,592	16.6
Hood	2	244	3,163	417.3	2,746	3,580	13.2
Hood	3	426	4,089	762	3,327	4,851	18.6

Table 3. Uncorrected pup production estimates for separate strata. Stratum 1: March 27, southern part, Stratum 2: March 28, northern part, northward, Stratum 3: March 28 southward at 2 nm spacing, Stratum 4: Strata 2 and 3 combined, 1 nm spacing, Stratum 1+4: Strata 1 and 4 combined.

Species	Stratum	Count	N	SE	lowerCI	upperCI	CV
Harp	1	2,255	30,393	10,186.6	20,206	40,580	33.5
Harp	2	1,394	18,217	5,691.9	12,525	23,909	31.2
Harp	3	1,770	23,322	5,036.5	18,285	28,359	21.6
Harp	4	3,164	20,629	3,556.5	17,073	24,185	17.2
Harp	1+4	5,419	53,101	9,049.4	44,052	62,150	17
Hood	1	413	5,540	1,297.5	4,243	6,837	23.4
Hood	2	325	4,254	1,437.3	2,817	5,691	33.8
Hood	3	260	3,436	732.5	2,704	4,168	21.3
Hood	4	585	3,824	753.1	3,071	4,577	19.7
Hood	1+4	998	9,775	1,471.8	8,303	11,247	15.1

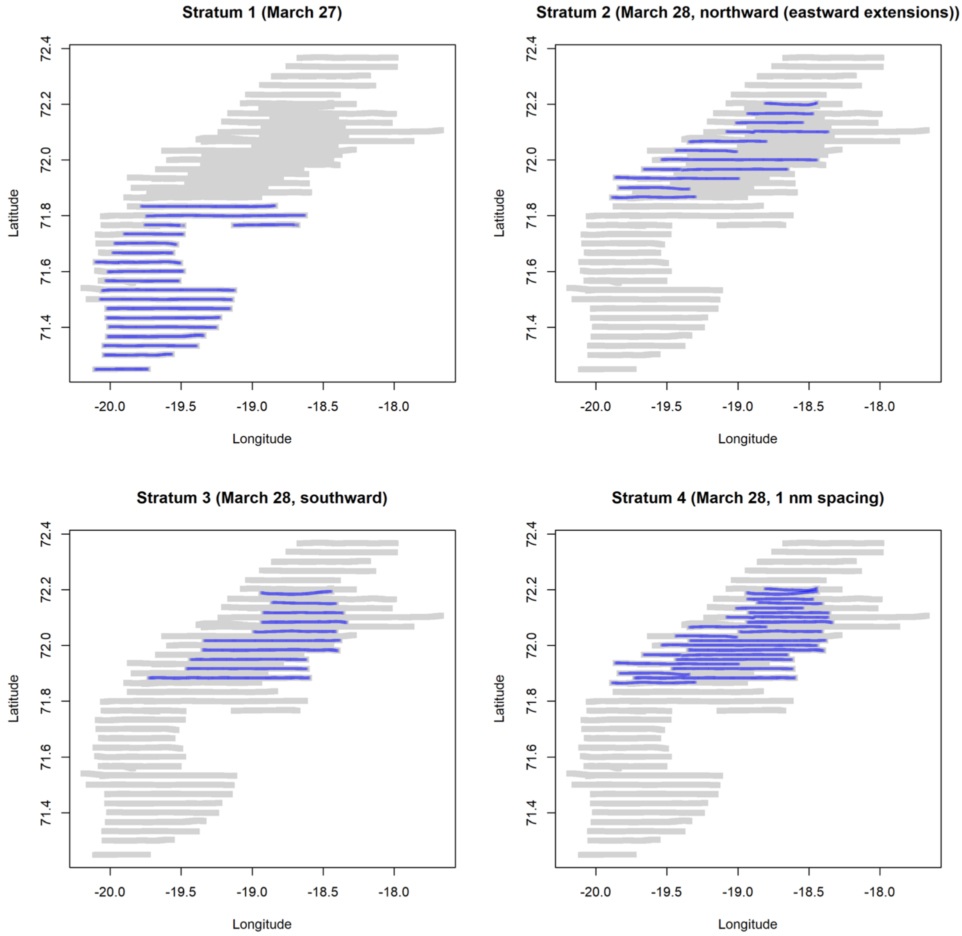

Figure 6. Maps showing the distribution of photographs designated to the four modified strata (blue), overlaid on all surveys combined (grey).

DISCUSSION

The 2018 surveys presented here provide the most recent estimates of pup production of harp and hooded seals in the Greenland Sea, and were carried out to ensure that the population assessment meets the previously established ICES criteria for considering the data input satisfactory (i.e., a time series of at least three pup production estimates spanning a period of 10–15 years where the last survey should not be more than 5 years old, ICES 2006a). The survey methods used during these surveys are comparable with those applied in previous pup production surveys of harp and hooded seals in the northwest Atlantic (Bowen et al., 1987, 2007; Hammill et al., 1992; Stenson et al., 1993, 1997, 2003, 2005, 2010; Stenson, Hammill, Kingsley, Sjare, Warren, & Myers, 2002), Greenland Sea (Haug et al., 2006; ICES, 1998, 1999; Salberg et al., 2008, Øigård et al., 2014a, 2014b; Øigård et al., 2010; Øritsland & Øien, 1995) and White Sea (ICES, 2019; Potelov et al., 2003). In general, the survey design calls for at least one counting survey of every whelping patch, carried out using either direct visual or photographic counts. Primarily due to the scattered distribution of both species during the current study, no visual surveys were attempted, and only one complete photographic survey could be obtained. While several repeated surveys would provide a more robust estimate of pup production, this represents a very substantial additional logistic and economic challenge, and further increases the already substantial risks associated with extended manned flight operations in remote pack ice regions. While alternative survey methods, for instance using unmanned aerial vehicles or satellite imagery, are being explored, the vast expanse of the areas to be covered represents substantial challenges to both these techniques. Extended beyond line-of-sight operations using long-endurance unmanned aircraft are possible, but it will likely take several years before such technologies become operationally mature especially in harsh polar regions. Similarly, the number of individual high-resolution satellite images required to survey the entire breeding area renders this approach prohibitively expensive and technologically unfeasible for the foreseeable future.

The complex photographic survey design imposed by weather conditions and lack of complete coverage in a single day, may have led to both upward and downward biases in our population estimates. While every attempt was made during day 2 to target the assumed area that was missed during day 1, the complex patterns of ice drift between the two days made it extremely difficult to account for this drift when planning the day 2 survey lines. These pup production estimates should therefore be treated as minimum estimates, and a new survey is planned for 2022 to assess their robustness.

Harp seals

Previous (1987-1991) mark-recapture experiments (Øien & Øritsland, 1995) and aerial surveys carried out in 1991 (Øritsland & Øien, 1995), 2002 (Haug et al., 2006), 2007 (Øigård et al., 2010) and 2012 (Øigård et al., 2014b) suggested substantial year-to-year variations in pup production, but no clear trend over time (Figure 7). However, the 2018 estimate is the lowest obtained since aerial surveys were introduced in 1991, and only one other survey (1987) resulted in a lower estimate. While survey estimates over the last decade shows a clear declining trend, it is possible that the less frequent survey schedules since 1991 may have obscured possible year-to-year variations. The difference in mean estimates between 2012 and the current corrected estimate of 54,181 (SE=9,049, CV=17.0%) is significant (t=12.723, df=26, p<0.0001), suggesting a reduction in pup production in the Greenland Sea similar to the reduction observed in the Barents Sea and White Sea population after 2003 (ICES, 2019). There are currently plans to carry out a new survey in the Greenland Sea in 2022 to determine if this declining trend continues.

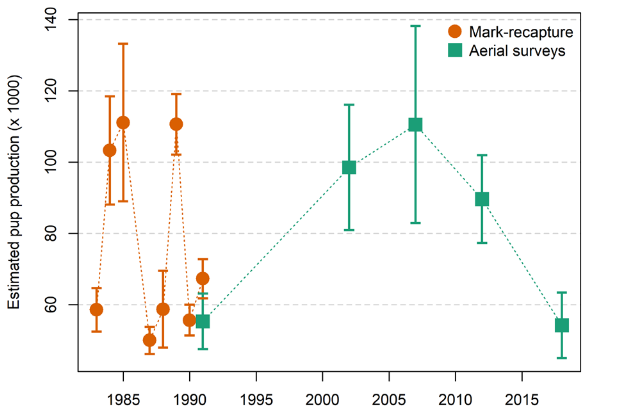

Figure 7. All pup production estimates obtained from harp seals since the start of surveys in 1977. Estimates based on mark-recapture experiments from 1977 to 1991 are shown in orange, while estimates based on aerial photo surveys are shown in green.

The switch between two methodologies for estimating pup production represents a potential issue when it comes to monitoring trends over time. Due to economic and logistical constraints, there is very little temporal overlap between these methodologies, which makes methods validation challenging. Furthermore, the mark-recapture estimates display substantial year-to-year variations, but it is unclear to what extent these indicate real variations, and to what extent they may represent potential biases in sampling, etc. While outside the scope of the present article, we plan to undertake a comprehensive review and re-analysis of the entire historical dataset, with special attention to potential environmental drivers that may help explain the substantial annual variability in the mark recapture estimates, as well as identify potential sources of measurement error in both methods.

Reconnaissance surveys were conducted in the period 18–31 March 2018 covering the entire latitudinal range historically used by harp seals in the Greenland Sea (areas between 68°40'N and 74°47'N, see Haug et al., 2006; Øigård et al., 2014b; Øigård et al., 2010; Øritsland & Øien, 1995). There is good evidence that previous ice conditions in the central Greenland Sea were significantly different from those witnessed in recent decades (Divine & Dick, 2006). These differences manifest themselves as a reduction in extent and concentration of drift ice, particularly within the region around and north of Jan Mayen Island, where the drifting ice traditionally formed an ice-peninsula (called Odden, see Wilkinson & Wadhams, 2005) which used to be the main harp seal breeding location (Sergeant, 1991). Observed ice reductions have obviously changed the harp seal breeding habitat in the Greenland Sea (Stenson et al., 2020): while the ice itself still appears to be suitable for nursing, the seals are now pupping on pack ice further west, within the East Greenland Current, which carries the ice (and the pupping area with it) quickly southward, rather than remaining relatively stationary north of Jan Mayen. It is important to note that the overall shift and contraction of the pack ice has been towards the west and the East Greenland coast, rather than towards the north. The shift in the location of pupping areas observed between the 1990s and the latest survey appears to follow this westward contraction, and there is no reason to suspect that there has been an overall displacement of pupping areas to regions outside of the latitudinal range covered by reconnaissance flights during the 2018 season.

These new conditions may have a negative impact on the first-year survival if they result in earlier loss of ice for the seals to rest on, or if the ecological conditions encountered by pups during the first few months of independent feeding differ from those encountered around the traditional area of Odden (north of Jan Mayen). Also, current pupping and breeding closer to the East Greenland coast may increase mortality of young and adults as they would be more vulnerable to predation from species such as polar bears (*Ursus maritimus*, Stenson et al., 2020). It is also possible that the reduced pup production is a result of reduced female reproductive performance, potentially linked to changes in prey abundance and distribution. Both adults and young Greenland Sea harp seals are known to migrate into the NW Barents Sea in large numbers (Folkow, Nordøy, & Blix, 2004; Rosing-Asvid et al., unpublished), where they often feed in waters associated with the retreating ice edge in summer and autumn. Large-scale changes to the Barents Sea system (e.g., Fossheim et al., 2015; Lind, Ingvaldsen, & Furevik, 2018), coupled with the westward contraction of the Greenland Sea ice edge, may have strongly influenced both the foraging performance and migratory distances between feeding and breeding areas, thereby negatively affecting the onboard energy reserves of pregnant females (Øigård, Lindstrøm, Haug, Nilssen, & Smout, 2013).

Whereas the Greenland Sea harp seal stock has been subject to commercial exploitation for centuries, the annual hunting pressure has been substantially reduced in the past 3–4 decades now amounting to, on average, less than 2% of the estimated total population (Haug, Stenson, Corkeron, & Nilssen, 2006; ICES, 2019; Iversen, 1927; Nakken, 1988; Sergeant, 1991). Based on catch per unit effort analyses and the mark-recapture pup production estimates from the 1990s and early 2000s, it was assumed that the population had been increasing since the early 1960s, although direct evidence of such an increase was limited (Ulltang & Øien, 1988; Øien & Øritsland, 1995). However, recent models (ICES, 2019) do suggest that the population may have increased in size since *circa* 1970, and results from previous assessments prior to the 2018 survey suggested that it could continue to increase under the very low harvest levels. Nevertheless, the 2018 pup production estimate is significantly lower than previous estimates, suggesting that the population may in fact not be increasing. As a result of including these most recent pup production estimates in the latest assessment carried out (ICES, 2019), the ICES/NAMMCO/NAFO Expert group on harp and hooded seals (ICES WGHARP) recommended a quota of 11,389 seals, down from a quota of 21,500 recommended in 2016 (ICES, 2016).

It is important to note that the annual fecundity rates in harp seals can be highly variable. In the Northwest Atlantic, where annual harp seal fertility estimates are available since 1954, the proportion of females that were pregnant undergoes dramatic variations, from 40% to more than 85% between years (Stenson, Buren, & Koen-Alonso, 2016; Stenson et al., 2020). Such changes can certainly account for rapid changes in pup production, which are therefore not necessarily an indication of a sudden population decrease or increase. In their most intensive feeding period during summer and autumn, Greenland Sea harp seals feed in the northern Barents Sea, an area subjected to a number of shifts in abundance of important fish species over time, and with a simultaneous collapse in important harp seal forage fishes such as capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) in the mid-1980s (Stenson et al., 2020). The more northern distribution of drift ice during summer and autumn in the last years may also have resulted in lower abundance and availability of important harp seal preys such as the pelagic amphipod *Themisto libellula*. The observed interannual fluctuations in mark-recapture pup production estimates for the years 1983–1991 may certainly have been driven by variations in female fertility caused by variable environmental conditions, although Øien & Øritsland (1995) suggested that these variations were the result of social associations affecting the distribution of marked pups in the breeding patches and that these recapture data might violate the assumptions underlying the mark-recapture methodology (Bowen & Sergeant, 1983). They also speculated that a mechanism of temporary emigration might have resulted in a bias in the estimates. Unfortunately, age at maturity and fecundity of Greenland Sea harp seal females have been only infrequently examined (see ICES, 2019), and data are insufficient to determine if reproductive rates have varied in this Greenland Sea population as they did in the Northwest Atlantic (Hammill, Stenson, Mosnier, & Doniol-Valcroze, 2021; Stenson et al., 2016; Stenson et al., 2020). Nevertheless, we plan to undertake a re-analysis of the entire pup production time series, which will examine any potential links between pup production and various large and small-scale environmental signals (e.g., North Atlantic Oscillation, local air pressure, ice conditions).

Hooded seals

Surveys using the same methodology as in the present study were conducted to also assess hooded seal pup production in the Greenland Sea in 1997 (ICES, 1999), 2005 (Salberg et al., 2008), 2007 (Øigård et al., 2010) and 2012 (Øigård et al., 2014a). The dramatic decline from 1997 (~24,000) to 2005/2007 (15,000-16,000, see Figure 8) led to a moratorium on catches from 2007 onwards. Despite a period of 11 years with no hunting, the corrected 2018 estimate (N=12,977, SE=1,823, CV=15.1%) is lower than all previous estimates although not significantly lower than the estimate in 2012 (t=1.462, df=26, p=0.136, Figure 8).

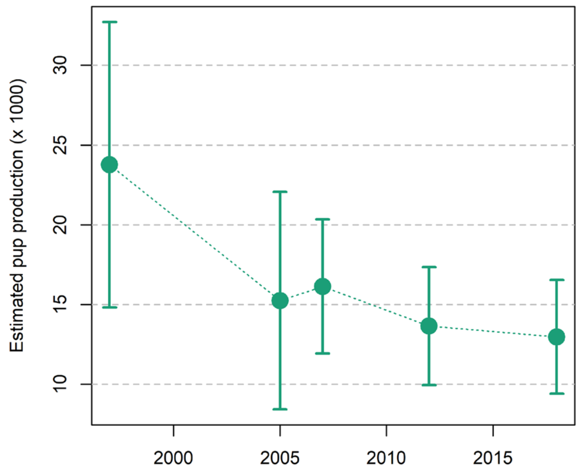

Figure 8. All pup production estimates for hooded seals, based on aerial photo surveys, since the start of surveys.

The accuracy of estimates obtained from aerial surveys is dependent on the degree to which the possible sources of error are minimised. In assessing the relative importance of different sources of bias when estimating seal abundance from aerial surveys, Myers & Bowen (1989) concluded that the greatest source of bias arose from missing whelping concentrations. Hooded seals are usually found in lower densities than harp seals (Lavigne & Kovacs, 1988) which may make them difficult to find. The extensive reconnaissance conducted in the period 18–31 March of all areas historically used by hooded seals in the Greenland Sea reduced the likelihood of missing major whelping concentrations in 2018, although difficult weather conditions may have left some pups unsurveyed in the very open ice fringes northeast of the area. In previous hooded seal surveys, the surveyed areas have traditionally consisted of three strata types: (1) concentrations, i.e., whelping patches where both visual and photographic surveys were conducted with high-density coverage, (2) scattered pups in areas of historically high pup densities, and (3) scattered pups in areas of historically low pup densities, with low-density photographic surveys being deemed sufficient in the latter two conditions (Bowen et al., 1987; Stenson et al., 1997). As was the case also in 2005 and 2012, hooded seal pups were scattered throughout the harp seal whelping patch also in 2018, with no sign of scattered pups outside of this area, and were therefore easily covered as part of the high-density coverage for harp seals. However, even low densities of pups spread over large areas can make a significant difference in the estimates of a small population.

Our results further support earlier suggestions regarding the historical changes in the hooded seal population in the Greenland Sea (Øigard et al., 2010). Changes in the size of harvested seal populations are often attributed to hunting pressure. Although the Greenland Sea stock of hooded seals has been subject to commercial exploitation for centuries (Iversen, 1927; Nakken, 1988; Sergeant, 1966), the hunting pressure was substantially reduced in the 2–3 decades that preceded the total protection of the species in 2007 (ICES, 2019; Salberg et al., 2008). However, despite the initially reduced and from 2007 complete stop in hunting, model runs using recent pup production estimates as input suggest that the Greenland Sea hooded seal population has decreased substantially since the 1950s and stabilised at a very low level (less than 10% of the

1946 level) since the 1970s (ICES, 2006a, 2019; Øigård et al., 2014a). So far, the total protection given to the stock in 2007 seems not to have resulted in any changes in population development. In other commercially harvested seal stocks in the North Atlantic (hooded seals in the Northwest Atlantic, harp seals in both the Northwest and Northeast Atlantic), models have indicated that reduced catches were followed by population increases from the early 1970s (Hammill & Stenson, 2005, 2006, 2007, 2010; ICES, 2006b, 2006a, 2019; Skaug et al., 2007). It seems unlikely that the different population development following reduced removals in Greenland Sea hooded seals could have been caused by recent hunting pressure alone (Øigard et al., 2010). The reduced hooded seal abundance also does not appear to be associated with any obvious reductions in female fertility (ICES, 2016) which has been observed in Northwest Atlantic hooded seal females (Frie et al., 2012).

The at-sea distribution area of Greenland Sea hooded seals includes virtually all of the Nordic Seas (Greenland, Norwegian and Iceland Sea, see Folkow, Mårtensson, & Blix, 1996; Vacquie-Garcia et al., 2017), which are dynamic ecosystems influenced by a combination of factors that will have to be considered simultaneously to explain the observed population development. The increase in water temperature and reduced ice cover in the Nordic Seas have resulted in a change in distribution and abundance of a number of fish species (Stenson et al., 2020). Several southern species, such as Atlantic mackerel (*Scomber scombrus*) and haddock (*Melanogrammus aeglefinus*) have extended their range northwards, while capelin, a dominant northern pelagic species, has retreated from Iceland towards the colder east Greenland waters. Atlantic cod (*Gadus morhua*) and beaked redfish (*Sebastes mentella*) are now found in Northeast Greenland while, in contrast, warming waters has led to a decline in the abundance and distribution of many cold-water species such as polar cod which use sea ice for spawning and feeding.

The observed reductions in extent and concentration of drift ice have obviously affected the hooded seal breeding habitat in the Greenland Sea in the same way it has for harp seals (see Stenson et al., 2020), with potential consequences for pup survival.

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