PUP PRODUCTION OF HARP SEALS IN THE NORTHWEST ATLANTIC IN 2017 DURING A TIME OF ECOSYSTEM CHANGE

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ABSTRACT

Photographic and visual aerial surveys were conducted off Newfoundland and Labrador ("the Front"), and in the Gulf of St. Lawrence ("Gulf") in March 2017 to estimate pup production of Northwest Atlantic harp seals (*Pagophilus groenlandicus*). Traditionally, harp seals pup (*whelp*) in three general areas; the southern Gulf of St. Lawrence, the northern Gulf of St. Lawrence, and off the east coast of Newfoundland and Labrador. After extensive reconnaissance, four whelping areas were identified: one in each of the southern and northern Gulf, and two at the Front. We estimated a total pup production in 2017 of 746,500 (SE=89,900, CV=12%), the lowest since 1994. Most (96%) pups were born at the Front (714,600 pups, SE=89,700). Very few pups were born in the southern Gulf (18,300, SE=1,500) and no whelping concentrations were observed prior to March 5, approximately 1 week later than previously observed. This is far lower than the 2012 survey estimate of 115,500 (SE=15,100) for the same area. Pup production in the northern Gulf was also lower than in previous years, at 13,600 (SE=3,000). The timing of births in the southern Gulf was much later than normal in 2017, and unusually early pupping at the Front suggests that some females from the Gulf herd may have moved to the Front to whelp due to a lack of ice suitable for pupping (i.e., thin first year) in the Gulf. Harp seals whelp in large concentrations. While one large whelping concentration formed at the Front, approximately 15% of the pupping at the Front occurred in small, dispersed groups which formed later than observed in previous years. Given the unusual ice conditions, distribution of whelping seals, and timing of pupping, assessing the results of the 2017 surveys relative to other estimates of pup production in the Northwest Atlantic is challenging and indicates the ongoing difficulties of assessing a population that is being impacted by climate change.

Keywords: Harp Seal, Pagophilus groenlandicus, pup production, survey, abundance, timing of births, Northwest Atlantic, sea ice, climate change

INTRODUCTION

Population abundance and trends are central themes in population ecology, management and conservation efforts. These parameters depend on the underlying vital rates such as production of offspring, juvenile and adult survival, immigration and emigration, which in turn are affected by a combination of density-dependent and density-independent (environmental) factors (Gaillard, Festa-Blanchet, & Yoccoz, 1998; Troyer, Devitt, Sunquist, Goswami, & Oli, 2014). One of the most important density-independent factors driving current ecosystem change in Arctic and sub-Arctic areas is global climate change. Climate change is impacting a variety of environmental variables including temperature, ocean circulation, pH balance, ice cover, and sea level (McCarthy, Canzani, Leary, Dokken, & White, 2001; Walsh, 2008; Intergovernmental Panel on Climate Change [IPCC], 2014; Haug et al., 2017). While a number of studies have examined the potential impact of this changing ecosystem on marine mammals in the Arctic (e.g.; Learmonth et al., 2006; Laidre et al., 2008; Kovacs, Lydersen, Overland, & Moore, 2011), relatively few studies (e.g.; Sundqvist, Harkonen, Svenson, &

Harding, 2012; Stenson & Hammill, 2014; Stenson, Haug, & Hammill, 2020) have examined impacts of climate change on sub-Arctic populations, although the changes associated with climate change are likely to be most rapid along the ice edge that they inhabit (Walsh, 2008). Alone, or in combination, the changes in environmental factors can lead to significant changes in the ecosystems that may be reflected in changes in foraging or birthing distribution, and abundance of populations.

For many species, direct counts to estimate abundance are not possible either because the population is distributed widely over an extremely large area, or because the entire population may not be visible at any one time. This has often led to the development of indices where the abundance of a subcomponent of the population is estimated, and then combined with other information to estimate total abundance. The pinniped life-history strategy is characterised by a period of marine foraging followed by a shorter period where animals must haul out on a solid surface (land or ice) to give birth and raise their young. Many pinnipeds often breed in colonies and

the pupping season is highly synchronised, providing a window of opportunity for surveys to be completed to estimate total pup production. Total abundance can then be estimated from a population model that incorporates data on pup production, reproduction rates, mortality, and removals (e.g.; Hammill and Stenson, 2011; Hammill, Stenson, Doniol-Valcroze, & Mosnier, 2015; Hammill, Stenson, Mosnier, & Doniol-Valcroze, 2021). However, estimates of pup production are important on their own as indicators of changes in abundance, early pup mortality, and distribution; each of which can be impacted by ecological changes.

Harp seals (*Pagophilus groenlandicus)* are the most abundant marine mammal in the North Atlantic. Three populations are recognised based upon their pupping (*whelping*) locations; the White Sea/Barents Sea population, the Greenland Sea population, and the Northwest Atlantic (NWA) population. As an abundant predator with a diverse diet, harp seals play an important role in stabilising their ecosystem and influencing the dynamics of their prey (Stenson, Haug, & Hammill, 2020). However, since harp seals are an obligatory ice-dependent species that rely on pack ice for at least part of the year and are abundant, high-trophic-level predators, they are also important indicators of ecosystem change (Conservation of Arctic Flora and Fauna [CAFF], 2017; Department of Fisheries and Oceans [DFO], 2012; Laidre et al, 2008; Kovacs & Lydersen, 2008; Stenson, Buren, & Koen-Alonso, 2016; Stenson, Haug, & Hammill 2020).

The largest population of harp seals is found in the Northwest Atlantic (International Council for the Exploration of the Sea [ICES], 2019). Throughout much of the year, Northwest Atlantic harp seals are widely distributed throughout Davis Strait, Baffin Bay, Lancaster Sound, Hudson Strait, and along the coast of Greenland, and thus are not available to be counted. However, beginning in fall, animals migrate south for pupping on the pack ice off the southeast coast of Labrador — an area known as "the Front" — and in the northern and southern Gulf of St. Lawrence ("Gulf") (Sergeant 1991; Stenson, Haug, & Hammill, 2020).

Harp seals rely on pack ice to haul out on, to give birth and nurse their young, and to moult. They rarely haul out on land. Whelping normally occurs on ice pans that are extensive enough to dampen wave action and thick enough to resist destruction from storm activity (i.e., first year ice with 6+/10 ice cover), while still allowing adults access to water (Bajzak, Hammill, Stenson, & Prinsenberg, 2011). Harp seals are social animals and form concentrations (often referred to as *patches*) to pup. Each year, NWA harp seals give birth on the pack ice off the coast of southern Labrador/Northeast Newfoundland ("the Front") and in both the southern ("Gulf") and northern ("Mecatina") Gulf of St. Lawrence.

Female harp seals mature sexually between three and seven years of age with almost all being sexually active by eight years of age (Stenson, Buren, & Sheppard, 2020). Females begin pupping in late February in the southern Gulf, and in early March in the northern Gulf and at the Front (Sergeant, 1991; Stenson et al., 1993; Stenson et al., 2002; Stenson, Rivest, Hammill, Gosselin, & Sjare, 2003; Stenson, Hammill, Lawson, Gosselin, & Haug, 2005; Stenson, Hammill & Lawson, 2011; Stenson, Hammill, Lawson, & Gosselin 2014). Pups are nursed for approximately 12 days, during which they remain on the ice and are visible to be surveyed in order to obtain estimates of pup production. Following weaning, pups undergo a three-week post-weaning fast during which they spend a considerable amount of time on the ice and are still reliant on ice for resting (Sergeant 1991; Stenson & Hammill 2014).

Prior to 1990, annual pup production was estimated using a variety of methods, including variations on a sequential population analysis approach, mark-recapture tagging, and aerial surveys (Sergeant 1975; Benjaminsen & Øritsland 1975; Winters 1978; Cooke 1985; Lavigne, Innes, Kalpakis, & Ronald, 1982; Bowen & Sergeant 1983). Since 1990, aerial survey methodology has become the preferred assessment approach and surveys have been completed at 4–5-year intervals since then. The aerial survey approach involves extensive reconnaissance of all ice suitable for whelping, to locate the seal concentrations and to deploy beacons for the monitoring of ice movement. Multiple surveys are carried out throughout the nursing period to determine the temporal distribution of births, and to count the number of pups born, using photographic and/or visual survey methods.

A review of the different estimates concluded that pup production in 1978 was in the order of 300,000–350,000 (Northwest Atlantic Fisheries Organization [NAFO], 1981). In 1990, pup production was estimated to have risen to 578,000 (SE=39,000) (Stenson et al., 1993). By 1999, it had increased to 997,900 (SE=102,100) (Stenson et al. 2002, 2003). Since then, pup production has varied considerably from 1.6 million (SE=110,000) in 2008 to 815,900 (69,500) in 2012. It should be noted that this latter estimate has been revised from the 791,000 (SE=69,700) reported previously due to additional analysis of survey transects that had not been completed at the time of the last assessment that was carried out in 2013 (Stenson et al., 2005, 2011, 2014, unpublished data).

The last estimate of NWA harp seal pup production was based upon surveys carried out in 2012 (Stenson et al., 2014). It was noted that the estimated number of pups born was significantly less than previously estimated in 2008 and that the proportion of pupping that occurred in the southern Gulf had declined, which is consistent with the trend in reduced ice extent observed in this area (Bajzak et al., 2011; Stenson & Hammill, 2014). The objective of this study was to estimate the number of harp seal pups born in the Gulf of St. Lawrence and off the northeast coast of Newfoundland and Labrador in 2017 with the same survey approach as used previously to determine if the trend observed in the 2012 survey had continued.

MATERIALS AND METHODS

Identification of whelping areas

Whelping concentrations were located using fixed-wing and helicopter reconnaissance flights over suitable ice in areas historically used by harp seals (Figure 1). At the Front and in the northern Gulf of St. Lawrence, fixed-wing reconnaissance flights were conducted almost daily (weather permitting) from March 6–18, 2017. Generally, repeated systematic east-west transects, spaced 18.5 km apart, were flown at an altitude of approximately 230 m, and extended from the shoreline or
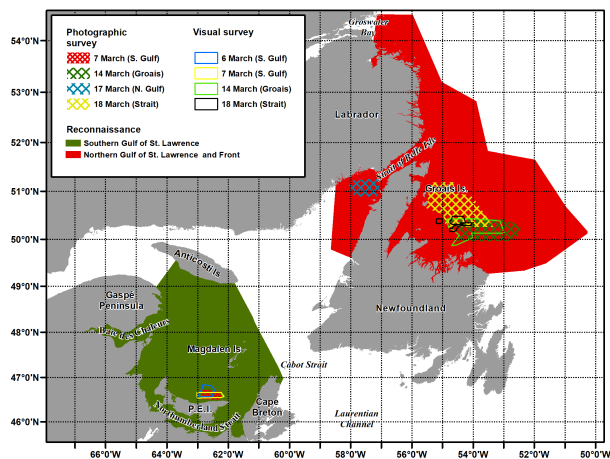
Figure 1. Reconnaissance and locations of whelping concentrations identified during the 2017 Harp Seal survey.

coastal edge of the ice pack, to the seaward edge between 49°30'N and 55°00'N at the Front and between the Strait of Belle Isle (~51°50'N) and the southern edge of the ice at approximately 49°45'N in the northern Gulf.

In the southern Gulf, reconnaissance surveys of areas traditionally used by harp seals were flown from February 28 to March 10, 2017. Because of the small amount of ice present in the traditional areas around the Magdalen Islands, fixed-wing flights were carried out throughout the southern Gulf from Cape Breton to the Baie des Chaleur, and northward to the Laurentian Channel and Anticosti Island (Figure 1). Information on the location of whelping seals was also gathered during helicopter reconnaissance flights and fixed-wing overflights conducted by Fisheries and Oceans Canada (DFO) Conservation and Protection Branch.

All areas were searched repeatedly to minimise the chance of missing whelping concentrations. Once located, satellite-linked beacons were deployed on the ice within each whelping concentration to monitor their movements as the pack ice drifted during the survey period.

Estimates of abundance

Harp seal pup production was estimated using strip transect survey methodology (Stenson et al., 1993, 2002, 2003, 2005, 2011, 2014). Surveys were carried out using visual (from helicopters) and/or photographic observations (from fixed-wing aircraft). The timing of surveys was chosen to maximise the number of pups present (i.e., most pups had been born) while taking into consideration ice conditions and predicted weather.

Surveys were designed based upon reconnaissance flights and estimated ice drift to maximise the number of transects that could be obtained and to ensure that an entire whelping concentration was covered on the same day. If necessary, the limits of the survey area were modified during the surveys to account for ice conditions, drift, and the location of seals on the day of the survey.

Visual surveys

Visual aerial surveys were flown using two Bell 429 helicopters at the Front and northern Gulf, and one in the southern Gulf of St. Lawrence, flying at an altitude of 61 m. Two observers seated

in the rear of each helicopter counted all pups within a pre-measured 30 m strip on each side of the aircraft (i.e., a total strip width of 60 m). Correct altitude and transect spacing were maintained using radar altimeters and GPS navigation systems.

Each observer recorded pup presence within the survey strip using a dedicated laptop system. The laptops ran custom survey software which was linked to GPS receivers so that each pup entry was georeferenced and assigned a time stamp. The software stored a summary of the pup counts for each transect, along with information on transect number, observer identity, weather, and other survey variables.

Visual surveys were carried out in the Gulf on 6 and 7 March, while surveys at the Front took place on 14 and 18 March. Additional surveys were carried out on 10, 13 and 22 March, but these did not cover all of the seals in the area and so were not considered further.

Photographic Surveys

The 2017 fixed-wing aerial photographic surveys were flown using one aircraft (Piper Navajo) in the southern Gulf and two aircraft (Piper Navajo and Rockwell Turbo Commander 690) at the Front, as previously done in the 2012 harp seal survey (Stenson et al., 2014). Each aircraft was equipped with a single, downward-facing Vexcel digital camera, coupled to a high-capacity hard disc array. The cameras were fitted with lenses of 100 mm focal length, and mounted in hydraulically-actuated motion compensation frames designed to minimise the effects of aircraft pitch, roll, and yaw. The CCD sensors collected black and white, and colour information in each image.

All surveys were flown at 110 knots and an altitude of 330 m. At this height, both cameras yielded image footprints on the ice of approximately 215 m along the flight line and 325 m across the flight line. The exact size of the area covered was estimated from each georeferenced image file to ensure accuracy. The digital cameras had a resolution of approximately 2.4 cm for objects on the ground at this height. A subset of images was reviewed during flight and technicians adjusted camera settings as needed to maximise image quality.

Photo intervals were chosen to obtain non-overlapping sequential frames along each transect line. However, in the southern Gulf, overlap occurred on some transects. In this case, seals were only counted in the overlap area on one frame to ensure that no pups were counted twice. Coverage along a line was generally over 90%, with the exception of the southern Gulf where overlap occurred (and therefore coverage was 100%), and the northern Gulf where coverage along a line varied between 75% and 93% (average 78%). Transect lines were spaced at 1.85 to 7.4 km apart depending on the configuration of the seal patch. If transect spacing changed within a survey, at least three adjacent lines at equal spacing were obtained to allow for variance estimation (see below).

Cameras were turned on before seals were encountered on a transect line and turned off if no seals were observed for an extended period along a transect line (>15 km) or if open water was encountered. This reduced the number of images that had to be analysed. Most transects ended when ice suitable for pupping was no longer available.

The southern Gulf harp seal whelping concentration was photographed on March 7. Transects were oriented in a north-south direction.

Photographic surveys of the Front concentrations ("Groais Island" and "Strait", Figure 1) were carried out on March 14 and 18, while the northern Gulf concentration was surveyed on March 17. Another photographic survey was carried out on March 19 with the intention of obtaining a second photographic estimate of the Groais Island concentration, but due to uneven ice drift, part of the concentration was missed, and the survey result was not used. All photographic transects were oriented in an east-west direction.

A total of 26,781 photos were taken. However, only 14,926 were used in the analysis, 2,233 from the southern Gulf and 12,693 frames from the northern Gulf and Front. The additional frames were taken during the incomplete survey on March 19 or along transects that overlapped with other surveys and therefore were not used to ensure that areas were not counted twice.

Correction for reader errors

The collected images were geo-referenced using the qGIS software (http://qgis.osgeo.org), and a virtual layer was superimposed on each photograph. Pup locations were marked by readers clicking on each pup they identified. The images were examined by five readers, one reader read all of the images from the southern Gulf surveys while four were involved in the reading of images from the Front and northern Gulf. To account for improvements in readings over time, after all photographs were examined each reader re-read the initial photographs in sequence until the counts from the first and second readings differed by less than 5%. If counts differed by more than 5%, the counts from the first reading were replaced by those from the second reading.

In order to ensure that pups are not missed on the images and that the counts from the readers were comparable, a series of 50 randomly-selected frames from each survey were examined by all readers. We then compared the *pups* identified and a *best estimate* of the number of pups present on the image determined. The best estimate (y_{ki}) was modelled as:

$$y_{ki} = a + bn_{ki} + u_{ki}$$

where n_{ki} is the initial count of the kth photograph by an individual reader i, a is the intercept, b is the slope, and u_{ki} is a random component that is normally distributed with zero mean and standard deviation σ.

In all cases, the intercept was not significantly different from zero and so the regression was repeated assuming a zero intercept. Because readers were restricted to different surveys, the photo counts for each survey were corrected using the appropriate estimate for the individual reader who read that survey.

$$\hat{n}_{ki} = \hat{b}n_{ki}$$

The measurement error associated with variation about the regression (V_{meas}) was estimated for each photo using the method described by Salberg, Haug, & Nilssen (2008). The measurement error for each photo was estimated by:

$$V_k^m = \hat{\sigma}^2 + var(\hat{b})n_k^2$$

where σ^2 is the estimate of the variance of the random component u, estimated as the variance of the residuals of the regression equation. The measurement error for the entire survey is:

$$V_i^m = W_i^2 \left[\sum_{j=1}^{J_i} \left(\frac{l_j}{F_j} \right)^2 P_j \hat{\sigma}^2 + var(\hat{b}) \left(\sum_{j=1}^{J_i} \frac{l_j}{F_j} \sum_{k=1}^{P_j} n_k \right)^2 \right]$$

where F_j is the total length of photos on a transect (i.e.,

$$F_j = \sum_{k=1}^{P_j} f_{j,k}$$

), $f_{j,k}$ is the length of photo (k) in transect j, P_j is the total number of photographs on transect j, l_j is the length of transect j, $W_i = S_i / w_i$, W_i is a weighting factor for the ith patch, S_i is the spacing between transects in patch i, and w_i is the width of the transects in patch i.

Survey analysis

Both visual and photographic surveys were based on a systematic sampling design with a single random start and a sampling unit of a transect of variable length. The basic survey design and analyses have remained the same since the surveys were first flown in 1990 with only some slight modifications (Stenson et al. 1993, 2002, 2003, 2005, 2011, 2014). The number of pups (N_i) for the ith survey was estimated by:

$$N_i = W_i \sum_{j=1}^{J_i} x_j$$

where x_j is the total number of pups on the jth transect.

For photographic surveys where frames did not overlap:

$$x_j = \frac{l_j \sum_{k=1}^{P_j} \hat{n}_{j,k}}{F_j}$$

If transect spacing changed within the survey area, each area of homogeneous transect spacing was treated as a separate survey (Kingsley, Stirling, & Calvert, 1985) with the estimated number of pups given by:

$$N_i = W_i \left[x_{i1} / 2 + \sum_{j=2}^{J_i-1} x_{ij} + x_{iJ_i} / 2 \right]$$

where J_i is the number of transects in the ith group, X_{ij} is the number of pups counted on the jth transect in the ith group, and the end transects are the limits of the survey area.

We estimated the variance of the survey based upon serial differences between adjacent transects using the method described by Salberg et al. (2008):

$$V_i^s = \frac{W_i J_i}{2(J_i-1)} \left(W_i - \frac{\sum_{j=1}^{J_i} F_j}{\sum_{j=1}^{J_i} l_j} \right) \sum_{j=1}^{J_i-1} (x_j - x_{j+1})^2$$

If transect spacing changed, the variance of each area of homogeneous transect spacing was given by:

$$V_i^s = \frac{W_i \left(W_i - \frac{\sum_{j=1}^{J_i} F_j}{\sum_{j=1}^{J_i} l_j} \right)}{2} \sum_{j=1}^{J_i-1} (x_j - x_{j+1})^2$$

The variance associated with the reader corrections V_i^m was added to the sampling variance V_i^s to obtain the total variance for a given survey V_i.

Estimates from two surveys of the same area were averaged (inversely weighted by their variance) using:

$$N_i = ((N_1 \times V_2) + (N_2 \times V_1))/(V_1 + V_2)$$

and its error variance:

$$V_i = (V_1 \times V_2)/(V_1 + V_2)$$

Temporal distribution of births

To correct the estimates of abundance for pups that were born after the survey had been flown, we estimated the temporal distribution of births during the pupping season. Based upon the developmental stages observed, it was assumed that the surveys were carried out before any pups had left the area. Occasionally pups were seen in the water, but because of their buoyancy they remained near the surface and were identified during the surveys. The proportion of pups in each of six age-dependent morphometric and pelage-specific stages was determined repeatedly throughout the whelping period (Stenson et al., 1993, 2002, 2003, 2005, 2011, 2014). A series of random, low-speed, and low-altitude (<10 m) helicopter surveys were flown over each whelping concentration during which pups were assigned into a series of six developmental stages (*newborn*, *yellow*, *thin whitecoat*, *fat whitecoat*, *raggedy-jacket*, or *beater*) based upon their size, colour, and shape (Stewart & Lavigne 1980). Due to the extremely short duration and subsequently small number of pups observed in the newborn and yellow stages, these two categories were combined into a single group called *newborn*. The change in proportion of newborn, thin whitecoat, and fat whitecoat pups over time was used to estimate the distribution of births. Stage durations for newborns (μ=2.40 days, SD=0.49 days, n=106), thin whitecoats (μ=4.42 days, SD =0.70 days, n=26), and fat whitecoats (μ=11.39 days, SD=1.22 days, n=80) were obtained from Kovacs & Lavigne (1985).

The temporal distribution of births was determined assuming that the timing of births followed a normal distribution and is described in detail by Stenson et al. (2003).

To correct for pups that had not been born by the time of the survey, the number of pups present on the ice were corrected by:

$$N_i = N_{uncor}/Q_i$$

where

N_{uncor} is the uncorrected estimate for survey i and Q_i is the proportion of births estimated to have occurred prior to survey i.

The estimates of N_{uncor} and Q_i are independent and therefore the error variance of the quotient is given by (Mood et al., 1974):

$$V_i = \left(N_{uncor}^2 \times V_p/Q_i^4\right) + V_n/Q_i^2$$

where V_p is the variance in the proportion estimated to have been present prior to survey i and V_n is the variance in the uncorrected estimate for survey i.

The total population was estimated as $\hat{N} = \sum_{i=1}^{I} N_i$ and its error variance $\hat{V} = \sum_{i=1}^{I} V_i$ where I is the number of surveys.

RESULTS

Identification of whelping areas

Total ice cover, and particularly first-year ice cover, was extremely low in the southern Gulf during February and March 2017 (Figure 2). The ice cover in 2017 was one of the lowest since records began in 1969. Although reconnaissance flights began on February 28, only occasional single harp seals were seen before March 5 when a concentration was located north of Prince Edward Island (PEI) (Figure 1). During the nursing period, the ice drifted eastward towards Cape Breton Island and then northward and out through the Cabot Strait (Figure 3).

Total ice at the Front was also below the long-term average (Figure 2). It was similar to the ice cover observed during the 2012 survey, but below that seen during the period between surveys. A whelping concentration was first observed on March 6 off northeast Newfoundland near the Groais Islands at approximately 51°00'N/55°00'W (Figure 1). Over the following week, this concentration increased in size and area as it spread outward to the east as the ice drifted and dispersed. A number of smaller concentrations (collectively referred to as "the Strait") were also identified to the north of the large Groais Island patch, originally to the east of the Strait of Belle Isle. Each of these patches was small and separated by the occasional scattered seal. Movement of each of the concentrations was monitored through the use of satellite linked GPS transmitters on the ice (Figure 3). Reconnaissance to the north of these concentrations continued until March 18. No additional pupping concentrations were found.
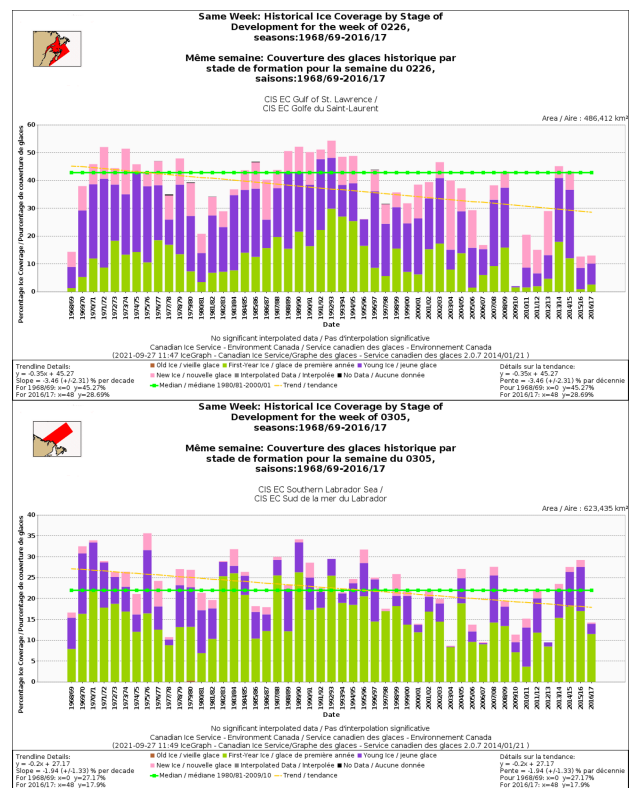

Figure 2. Historic ice cover (1969-2017), by type, in the southern Gulf of St. Lawrence (top, week of February 26), and off southern Labrador (bottom, week of March 3). Harp Seals prefer first year ice.
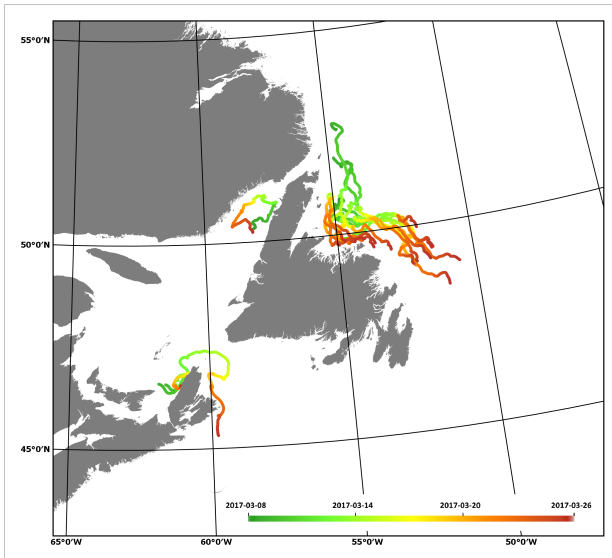
Figure 3. Movement of satellite-linked GPS transmitters deployed in whelping concentrations to monitor ice movement during the March 2017 Harp Seal survey.

A small concentration of seals was located in the northern Gulf on March 6 at approximately 50°20'N/58°15'W (Figure 3). Strong southerly winds forced the ice the seals were on northward and then it drifted southward, ending up very close to where it started three weeks earlier. However, this ice broke up and became quite dispersed during this period.

Pup production surveys

Reader corrections

Correction factors for photographic surveys were developed for all readers. The regressions of the best counts on the individual reader counts were significant and since all of the intercepts were not significantly different from zero, they were recalculated assuming a zero intercept. The fit to the regressions was good with corrections ranging from approximately 1–8% (Table 1). There was very little difference between the counts of the five readers for all of the images examined.

Survey estimates

Southern Gulf

In the southern Gulf, the herd was delimited and visual surveys were flown on March 6 and 7. A total of 915 pups were counted on the 20 east-west transects flown on March 6 (Figure 4A), resulting in an estimated total number of pups present on the ice of 17,216 (SE=3,685; CV=21%; Table S1). A second survey, consisting of 13 east-west transects, was flown on March 7 (Figure 4B). A total of 1,215 pups were recorded and the total number of pups was estimated to be 19,292 (SE=2,201; CV=11%; Table S2). A photographic survey was also flown on March 7. A total of 27 north-south transects were completed (Figure 4C), with 3,187 pups detected on 2,233 images, resulting in an estimated pup count of 16,768 (SE=2,322, CV=14%; Table S3). Averaging all three estimates, without correcting for the temporal distribution of births, resulted in an estimated number of pups present in the southern Gulf of St. Lawrence of 17,958 (SE=1,466; CV=8.2%).

Northern Gulf

The whelping concentration that was identified in the northern Gulf of St. Lawrence was surveyed photographically on March 17. The survey consisted of 12 east–west transects spaced at 3.7 km apart (Figure 5C). The southern transects covered areas of open water. A total of 768 pups were identified on 2,305 photographs, resulting in an estimated 13,597 (SE=2,953, CV=22%; Table S4) pups present at the time of the survey. Due to high winds and shifting ice, it was not possible to survey this patch a second time, neither visually nor photographically.

The Front

Groais Islands

Both visual and photographic surveys of the largest harp seal concentration off the northeast coast of Newfoundland were carried out on March 14 (Figure 5A). The visual survey consisted of 17 east-west transects carried out by two helicopters and separated into two sections with a transect spacing of 5.56 km and one section with transects spaced 2.77 km apart (Table S6). A total of 10,224 pups were counted resulting in an estimate of 554,505 (SE=95,219; CV=17%; Table S5) pups present on the ice. The photographic survey on March 14 was split into two segments. The first covered the area that had been surveyed visually. This survey was comprised of eight east-west transects spaced 7.4 km apart with a total of 25,713 pups counted on 4,083 photos (Table S7). The pups were clustered throughout the area and the total number of pups was estimated to be 586,170 (SE=193,252; CV=33%; Table S6). Averaging the two surveys resulted in an estimate of pup production on the day of the survey of 560,691 (SE=85,414; CV=15%).

Table 1. Regression statistics used to correct for misidentified pups on photographs. Each reader read a minimum of 50 photographs to develop the regression. The total number of photographs read, intercept, slope and adjusted R² are presented.

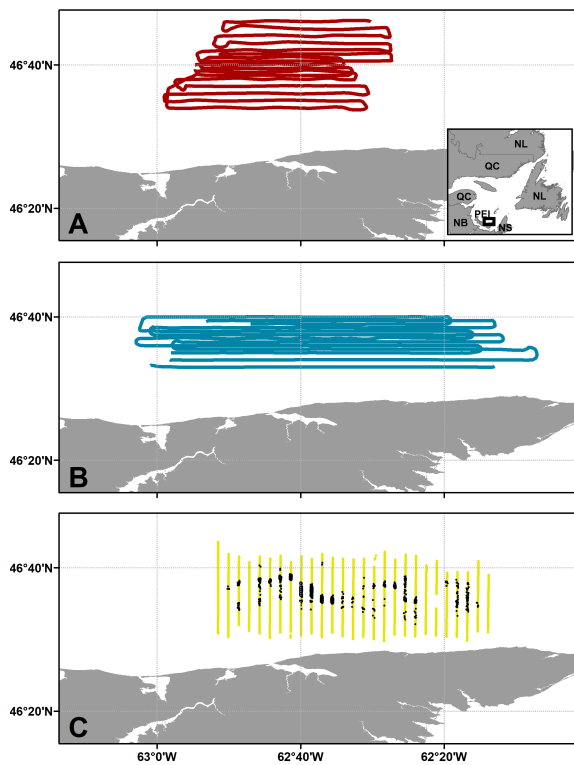| Area	Patch	Reader	Photos Read	Slope (SE)	R²	Random Error
Front	Groais Is.	BS	3,844	1.009 (0.002)	0.9999	0.366
Front	Strait	KM	6,405	1.086 (0.007)	0.9981	0.740
Front	N. Gulf	RC	2,305	1.028 (0.011)	0.9943	0.314
Font	Groais Is.	VH	139	1.016 (0.004)	0.9991	2.465
Gulf	S. Gulf	PR	2,233	1.041 (0.005)	0.999	0.764

Figure 4. Survey transects during the March 6 (A) and March 7 (B) visual surveys, and March 7 photographic survey (C). Black dots indicate the location of seals during the photographic survey.

A small section of ice containing harp seal pups was surveyed photographically only. This section was east of a large body of open water and could not be reached by the helicopters. No photographs were taken on the last transect which was open water. The number of pups present on the day of the survey in this group was estimated to be 50,373 (SE=22,477, CV=45%) based on three transects spaced 7.4 km apart (Figure 5A, Table S7). Adding this amount to the average of the two surveys of the rest of the concentration results in an estimated pup count for the entire concentration of 611,064 (SE=88,322; CV=14%).

Strait

A number of small, scattered patches formed north of a large Groais Islands concentration. While visual surveys of individual patches were carried out, not all were covered and the estimates could not be combined for a visual estimate of the full area. However, a large-scale photographic survey carried out on March 18 covered the area. This survey consisted of 19 transects with spacing of either 7.4 or 3.7 km (Figure 5B). A total of 6,898 pups were counted on 6,405 photos resulting in an estimated pup production of 101,484 (SE=15,630; CV=15%; Table S8) harp seals. This photographic survey missed one of the small patches that was surveyed visually on the same day. This survey consisted of 13 east-west transects spaced 926 m apart during which 133 pups were counted, resulting in an estimated of 2,053 (SE=253; CV=12%; Table S9). Combining the photographic and visual estimates resulted in a total estimated pup production prior to the surveys in the Strait area of 103,536 (SE=15,632; CV=15%).
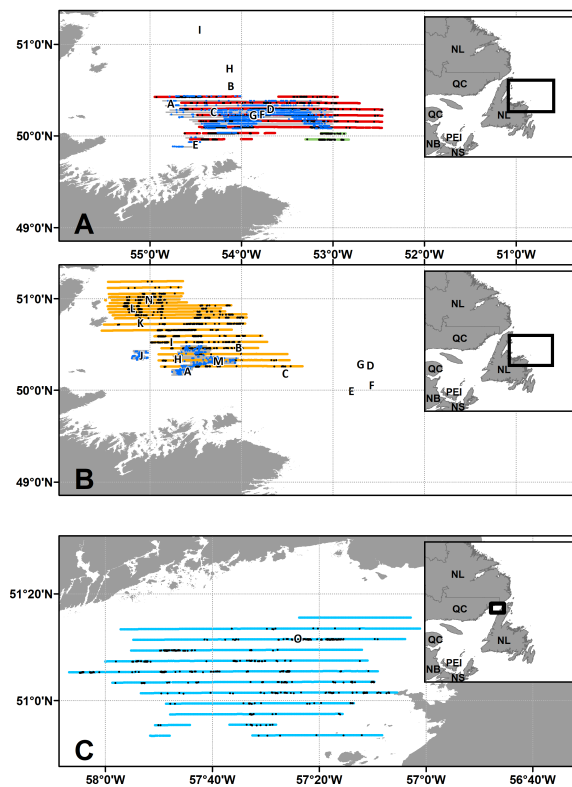

Figure 5. Survey transects of the Groais Island (A, 14 March), Strait (B, 18 March), and Northern Gulf (C, 17 March) whelping concentrations. Visual surveys are indicated by grey line while photographic surveys are in colour. The 'northern' Groais Island survey lines are red while the separate 'eastern' Groais Island transects are in green. Pups identified during visual surveys are shown in blue while pups identified on photographs are black. Letters refer to individual ice beacons to indicate drift.

Modelling the temporal distribution of births

Estimates of the proportion of pups in each of the developmental stages were obtained from all four whelping areas (Table S10). Staging surveys were carried out over the entire pupping and nursing period.

In 2017, pupping in the southern Gulf began later than in 2012 (Figure 6). In contrast, it began earlier in the Groais Island patch in 2017 than in 2012, but at the same time as in the southern Gulf. However, it continued later in Groais Island than the Gulf, ending at the same time as the Main patch during the 2012 survey. Pupping in the northern Gulf in 2017 was similar in timing to that seen at the Main (Front) and Belle Isle in 2012. In 2017, the Strait concentration appeared to form later than the other areas.

The estimated proportion of pups that were born at the time of the March 6 survey in the southern Gulf was 0.9632 (SE=0.0147) (Table 2). This increased to 0.9846 (SE=0.0071) by the next day when the photographic and second visual surveys were carried out. Although it is small, we did apply a correction for the estimate of pups born after the survey date to all three of these surveys.

The estimated proportion of pups born on the day of the survey was ≥0.999 for all three surveys off Newfoundland (Table 2).
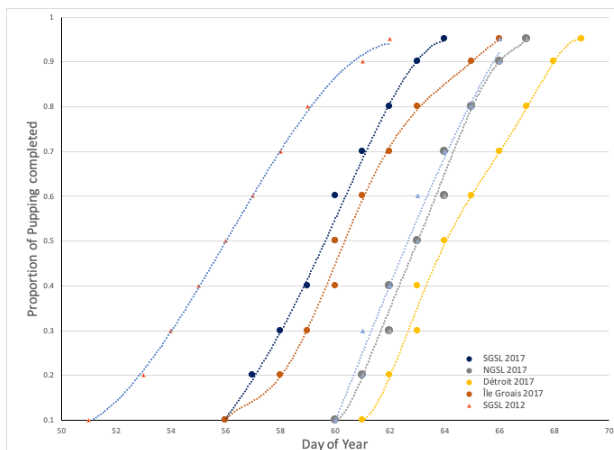
Figure 6. Proportion of pups born versus day of year in the four whelping concentrations in 2017 (circles), and three concentrations in 2012 (triangles).

Therefore, no correction for the temporal distribution of births was applied.

Estimating total 2017 pup production

Adjusting the visual survey estimates in the southern Gulf to account for births that had occurred after the survey had been flown resulted in visual estimates of 17,873 (SE=3,835) and 19,593 (SE=2,240) pups and a photographic estimate of 17,029 (SE=2,362) pups (Table 3). Averaging these three surveys results in an estimate of pup production in the southern Gulf of St. Lawrence of 18,302 (SE=1,496; CV=8.2%).

No corrections for pups born after the survey were applied to the northern Gulf, Strait or Groais Island concentrations. Therefore, combining the average estimate from the southern Gulf with those of the northern Gulf (13,597; SE=2,953, CV=22%), Strait (103,536; SE=15,632; CV=15%), and Groais areas (611,064; SE=88,322; CV=14%) resulted in an estimate of total pup production (rounded to the nearest hundred) in 2017 of 746,500 (SE=89,800, CV=12%) (Table 3).

DISCUSSION AND CONCLUSIONS

The methods used in this survey are essentially the same as those used to estimate pup production of harp seals since 1990 (Stenson et al. 1993, 2002, 2003, 2005, 2011, 2014) and so the results of the various surveys should be directly comparable. Usually, harp seals pup in relatively high-density *concentrations* within a larger area of suitable ice (Sergeant, 1991). Stenson & Hammill (2014) observed that pupping appears to occur in traditional areas even if ice conditions are poor and ice-related mortality may result. The only time pupping has been observed outside of these usual locations occurred when ice was completely absent during the period when the whelping concentration was forming up. Since missing whelping concentrations is the largest single source of error in a survey, extensive reconnaissance is carried out to detect all of the patches (Bowen, Myers, & Hay, 1987). Once located, we deployed satellite-linked GPS beacons on the ice to ensure that we can monitor ice movements so that all of the concentrations identified are surveyed and any duplicates are identified. This, for example, allowed us to determine that some of the smaller groups we surveyed visually on March 18 were also

photographed while one group was not. Because of the wide distribution of pupping and extensive ice drift that occurred in 2017, we used a total of 18 beacons to track the ice.

Once located, we carried out pup staging surveys to determine the temporal distribution of births within each concentration in order to correct the survey estimates for the proportion of pups present on the ice at the time. The timing of the pup production surveys is designed to maximise the numbers of seal pups present on the ice, although it must also take into account the weather, as well as the likelihood that the ice may not persist or that it will spread too extensively to be completely surveyed in a single day. As in the past, the reader's counts of seals on the photographic images were standardised and corrected for missed pups. The high-quality images we obtained had very good resolution at the survey altitudes used in this survey and as a result, the reader corrections were minimal.

With an estimate of 746,500 (SE=89,800), 2017 pup production of Northwest Atlantic harp seals was lower than it has been since 1994 (702,900, SE=63,600; Table 4) even though the population is estimated to have increased (Hammill et al. 2021). The 2017 pup production estimate is similar to estimates obtained in 2012 (815,900, SE=69,500) and 2004 (991,400, SE=58,200), but less than half of the 2008 estimate (1,644,500, SE= 117,900). The number of pups that are born in a given year will depend upon the number of sexually mature females in the population and the pregnancy rate of mature females. However, since the early 1980s, late-term pregnancy rates among mature females declined while interannual variability has increased, with rates ranging from 20% to over 85% (Stenson, Buren & Sheppard, 2020). Stenson et al. (2016) found that while the general decline in fecundity is a reflection of density-dependent processes associated with increased population size, the large inter-annual variability is due to varying rates of late term abortions which are, in turn, related to changes in capelin (*Mallotus villosus*, their main prey) abundance and mid-winter ice coverage. The Labrador and Newfoundland Shelves are important feeding areas for harp seals prior to pupping, both for seals that remain at the Front and for those that enter the Gulf (Sergeant, 1991; Stenson & Sjare, 1997). Capelin biomass off Newfoundland has declined significantly since the late 1980s and is impacted by changes in the timing of ice retreat which influences the timing of the primary productivity bloom and, as a result, the amount of zooplankton available as prey for capelin (Buren et al., 2014; Lewis, Buren, Regular, Mowbray, & Murphy, 2019; Buren et al., 2019). This suggests that the interannual variability in mid-winter ice extent reflects environmental conditions that influence a variety of harp seal prey species and subsequent seal pregnancy rates.

Pregnancy rates were particularly low in 2004 (38%), but much higher in 2008 (77%) while rates in 2012 and 2017 (61% and 58%, respectively) were close to the average pregnancy rate observed over the past decade (Stenson, Buren & Sheppard, 2020). If the number of mature females in the population was similar, variable pregnancy rates could account for much of the variation in pup production. This also suggests that the 2012 estimate was not unusually low, but rather that the 2008 estimate may have been unusually high. These varying estimates illustrate the difficulties of using a single measure such as pup production as an indicator of changes in abundance.

Table 2. Estimated proportions of Northwest Atlantic Harp Seal pups on the ice at the time of the surveys.

Area	Survey Type	Date	Estimate	Std. Err	Correction Applied
S. Gulf	Visual	March 6	0.9632	0.0147	Yes
-	Visual + Photo	March 7	0.9846	0.0071	Yes
Groais Is	Visual + Photo	March 14	0.9998	0.0002	No
Strait	Photos	March 18	0.9999	<0.0000	No
N. Gulf	Photographic	March 17	1.0	<0.0000	No

Table 3. Estimated pup production and standard errors of Northwest Atlantic Harp Seals during March 2017. The southern Gulf surveys are corrected for the estimated numbers of pups that may have been born after the survey. Estimates in bold are used in the final total.

Area	Date	Method	Estimate	Std Err	CV
S. Gulf	March 6	Visual	17,873	3,835	0.215
-	March 7	Visual	19,593	2,201	0.114
-	March 7	Photo	17,029	2,362	0.139
-	-	**Averaged**	**18,302**	**1,496**	**0.082**
N. Gulf	March 17	**Photo**	**13,597**	**2,953**	**0.217**
Groais Is. N	March 14	Photo	586,170	193,252	0.330
-	-	Visual	554,505	95,219	0.172
-	-	Averaged	560,691	85,414	0.152
Groais Is. E	March 14	Photo	50,373	22,477	0.446
-	-	**Total**	**611,064**	**88,322**	**0.140**
Strait	March 18	Photo	101,484	15,630	0.154
-	-	Visual	2,053	253	0.123
-	-	**Combined**	**103,597**	**15,632**	**0.151**
-	-	**Total**	**746,499**	**89,755**	**0.120**

Hammill et al. (2021) attempted to estimate total abundance using a model that incorporates the periodic estimates of pup production as well as annual estimates of age specific pregnancy rates and removals. After increasing from a low in the early 1970s, the population appeared to be stable from the mid-1990s until approximately 2014, due to a combination of high catches (particularly of young of the year) in both Canada and Greenland, reduced reproductive rates, and a series of years with high ice-related mortality of young of the year. Stenson & Upward (2020) found very few females from the 1996–2012 cohorts in their reproductive samples also suggesting that there may he been low survival over these years. Since 2014, however, the population was estimated to be increasing again as a result of several years with high reproductive rates and low mortality of young (Hammill et al. 2021). However, it would take several years, likely 6–10, before the impact of the reduced catches and improved survival of young seals propagate through the population as these cohorts become sexually mature and are reflected in pup production. Thus, any potential increase in the population would not be reflected in the 2017 pup production estimate.

In 2017, pup production in the southern Gulf was greatly reduced relative to previous surveys. Three surveys of the area resulted in an estimate of only 18,300 (SE=1,500) pups. This is in contrast to 2012 when 115,500 (SE=15,100) pups were born, and 2008 when pup production was estimated to be 287,000 (SE=27,600) (Table 4). The southern Gulf has traditionally accounted for 20-30% of the total Northwest Atlantic pup production, although the proportion has been declining since 2004. In 2017, however, only 2% of pup production occurred in

Table 4. Northwest Atlantic Harp Seal pup production estimates from aerial surveys completed since 1990 (with SE), and the proportion of pupping in each component.

Year	Southern Gulf	Northern Gulf	Front	Total	Reference
1990	106,000 (23,000)	4,400 (1,300)	467,000 (31,000)	578,000 (39,000)	Stenson et al. 1993
1994	198,600 (24,200)	57,600 (13,700)	446,700 (57,200)	702,900 (63,600)	Stenson et al. 2002
1999	176,200 (25,400)	82,600 (22,500)	739,100 (96,300)	997,900 (102,100)	Stenson et al. 2003
2004	261,000 (25,700)	89,600 (22,500)	640,800 (46,900)	991,400 (58,200)	Stenson et al. 2005
2008	287,000 (27,600)	172,600 (22,300)	1,185,000 (112,474)	1,644,500 (117,900)	Stenson et al. 2011
2012	115,500 (15,100)	74,100 (12,400)	626,200 (66,700)	815,900 (69,500)	Stenson et al. 2014, this paper
2017	18,300 (1,500)	13,600 (3,000)	714,600 (89,700)	746,500 (89,800)	this paper

Proportions

Year	Southern Gulf	Northern Gulf	Front	Total	
1990	0.18	0.01	0.81	-	
1994	0.28	0.08	0.64	-	
1999	0.18	0.08	0.74	-	
2004	0.26	0.09	0.65	-	
2008	0.17	0.11	0.72	-	
2012	0.14	0.09	0.77	-	
2017	0.02	0.02	0.96	-	
Average	0.18	0.07	0.75	-	
SD	0.08	0.04	0.11	-	

the southern Gulf, and the timing of births was also considerably later than observed previously.

There was very little ice, both in terms of extent and thickness, in the Gulf during 2017. This continues a trend that has been ongoing since the mid-1990s (Friedlander, Johnston, & Halpin, 2010; Bajzak et al. 2011; Stenson & Hammill, 2014). In 2017, only a small amount of ice was thick enough to support pupping harp seals. In late February, which is the traditional time for pupping to begin in the southern Gulf, a small amount of thin, newly frozen ice was present north of PEI and towards Cape Breton, while some heavier and thick ice that could support seals was present in Northumberland Strait. Reconnaissance flights covered this entire area on February 28 and again over the following days with no indication of pupping until March 5 (cf. late February previously). To determine if pupping was occurring in areas outside of the traditional southern Gulf pupping area, fixed wing reconnaissance flights examined all possible ice from the New Brunswick coast, into Baie des Chaleurs, and along the Gaspe Peninsula across to Anticosti Island. Reconnaissance flights out of Newfoundland covered the area in the northern Gulf. There were no reports of births on land, which is consistent with what we know about this species

(Stenson & Hammill 2014). Thus, there was no indication of pupping outside of the small group that was surveyed.

It is possible that some females gave birth on very thin ice that broke up prior to the surveys, although the extent to which this may have impacted the estimates is not known. If pupping did occur in late February on the limited ice that was present in their traditional area, the pups would have to have been lost prior to the reconnaissance on February 28 or missed on these flights and lost before the next flights that did not occur until March 3 due to poor weather. On March 5 a concentration of pups was located approximately 75 km to the north of Prince Edward Island, an area that was considered to be 9/10 ice covered. However, only 3/10 of that ice was considered to be suitable for pupping (Bajzak et al. 2011) while the rest was too thin (*grey white*) or simply *slush*. This concentration had not been detected prior to March 5, and was not seen after this date. Pups were later located off the northern shore of Prince Edward Island during photographic surveys March 6 and 7. If the patch of animals mentioned above drifted to the PEI coast, then mortality could have been high, due to high winds (gusts of over 80 km/h) recorded at the time. These conditions could have broken up the ice and cast pups into the water where they

would have drowned prior to the survey being flown. However, it is highly unlikely that this could account for all the differences observed between the 2012 and 2017 surveys.

Comparing historical locations of NWA harp seal whelping patches to observations made during two years (2010, 2011) of exceptionally low ice, Stenson & Hammill (2014) found that females pupped in their traditional areas if any amount of ice was present, even if the ice was too thin to sustain the pups and led to high pup mortality. Females only moved to more suitable ice outside of their traditional whelping areas if no ice was present within these traditional areas. In 2017, suitable ice did not form in the traditional southern Gulf whelping area around the Magdalene Island until early March, which is well after when pupping usually begins in this area. It is possible that some females from the southern Gulf moved northward towards better ice conditions to give birth.

Some suitable ice was present in the northern Gulf, near the Strait of Belle Isle, in late February, but it does not appear that large numbers of females pupped in this area. The number of pups born in the northern Gulf was also low (13,600, SE=3,000; cf. 74,100, SE=12,400 in 2012) and the temporal distribution of births in the northern Gulf was similar to that seen in 2012 in both the northern Gulf and at the Front.

The presence of fat whitecoats (~1–2 weeks old) at the Front on March 7 strongly suggests that some Gulf females moved to the Front to give birth. Traditionally pupping occurs later at the Front with very little pupping prior to March 5 or 6. In 2017, however, pupping appeared to have begun approximately four or more days earlier in the Groais Island patch, although it was more protracted and ended near the same date as in 2012. It appears that some early pupping, likely by southern Gulf females, created the nucleus of the whelping concentration that was joined later by Front females that pupped at their usual time, creating a second pulse of pupping. The number of pups born at the Front was higher in 2017 than in 2012 (714,800 versus 626,200, respectively), but what proportion of the southern Gulf females may have moved to the Front is unknown.

Harp seal females are thought to show site fidelity by returning to pup in the same area, presumably the one where they were born, each year (Sergeant 1991). However, it is unknown if any females that may have moved to the Front to pup in 2017 will stay there or return to the Gulf in future years or if pups from Gulf females who were born at the Front will eventually pup in the Gulf or the Front.

Sergeant (1991) reports a similar situation in 1969. That year, ice in the southern Gulf was restricted to Northumberland Strait and shore ice along the north coast of PEI. Approximately 40,000 pups were born in the area compared to the 100,000 who were thought to have pupped there the previous year. However, subsequent sampling did not show any reduction in the 1969 year class in the Gulf and, although there was no way to determine, it was speculated that females had moved north to the Front to pup. The staging data from 2017 provide some evidence that this may occur.

The Strait whelping area that was surveyed on March 18 consisted of a number of small pupping concentrations spread over a large area. None of these groups formed up into the typical large concentrations seen in previous year. The proportion of pups in the various developmental stages

indicated that the timing of pupping was similar in most of these groups and so could be combined, but the overall timing of pupping among these groups was later than in other concentrations observed in either 2017 or 2012. This indicates that, for some reason, pupping occurred later than normal among these smaller groups and raises the possibility that some pupping may have occurred after the survey period. The area covered during the March 18 survey was quite large and while it is possible that we may not have found some small groups that were outside of this area, these are unlikely to have been very large.

All suitable ice up to Grosewater Bay was examined both early in March and again later. Harp seal pups were found off southern Labrador during the early flights and drifted southward where they were included in the surveys. No whelping harp seals were observed north of the Strait group during the reconnaissance conducted on March 18. If there had been any pupping north of the traditional area, this ice would have drifted south (Figure 3) and been examined during flights in late March. This indicates that there was no pupping north of the traditional area in 2017.

Conclusions

Changes in pup production and the distribution of whelping among northwest Atlantic harp seals reflect the ecological changes occurring in their habitat and highlight the importance of harp seals as ecosystem indicators. Changing levels of pup production, early life history mortality and distribution of whelping sites all provide valuable information on how harp seals are influenced by environmental change. Pup production of northwest Atlantic harp seals during 2017 was similar to that of the previous survey carried out in 2012, but much lower than observed in 2008. Ice conditions were very poor in 2017, especially in the southern Gulf of St. Lawrence where only a very small number of pups were estimated to have been born. It appears that some of the Gulf females moved to the Front and there may have been some ice related mortality prior to the survey, but whether this can account for the >100,000 seals that had regularly pupped in the southern Gulf, even in years of very poor ice and high pup mortality, is not clear. The timing of pupping at the Front was also unusual in 2017. In addition to some very early pupping, there was also some late pupping in the more northerly areas. Given the timing of the surveys at the Front, it is possible that some of the early pups may have been weaned and left the ice prior to the survey, but given that relatively few seals had reached the *grey* stage at which weaning often occurs, it is unlikely to have accounted for a significant underestimate. Also, a significant amount of the whelping was distributed broadly in a number of small groups which are difficult to survey and it is always possible that some small groups were missed. Therefore, while the above unusual conditions in 2017 add to the uncertainty in survey results, available ice condition information and the efforts to address potential biases provide an estimate of pup production of harp seals in the northwest Atlantic that is comparable with previous surveys.

In the northwest Atlantic harp seals pup near the southern edge of the seasonal pack ice. Over the past three decades, this area has shown significant reductions in sea ice coverage and quality (Bajzak et al. 2011; Stenson & Hammill 2014; Laidre et al. 2015). Hammill et al. (2015) found that although ice cover varied considerably among years, there has been a significant declining

trend in annual ice cover in the Gulf of 1,940 km². While the decline in sea ice in the Gulf is easily recognised because of the overall lower amount of ice present, Stenson and Goulet (unpublished data) found that years with poor ice in the Gulf are highly correlated with poor ice at the Front. If the current warming trends continue, ice-breeding harp seals will encounter more years with poor ice conditions and may eventually adapt by moving north. Until then, they will continue to have increased levels of mortality that could result in the disappearance of the most southern breeding component in the Gulf of St Lawrence.

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national laws and protocols for animal welfare that are applicable in the jurisdictions where the work was conducted.

AUTHOR CONTRIBUTION STATEMENT

Garry Stenson: Conceptualisation, Planning, Data collection, Analyses, Writing - original draft; Jean-Francois Gosselin: Planning, Data Collection, Analyses, Writing – reviewing and editing; Jack Lawson: Conceptualisation, Planning, Data collection, Analyses, Writing – reviewing and editing; Alejandro Buren: Planning, Data collection, Analyses, Writing – reviewing and editing; Pierre Goulet: Data collection, Analyses, Writing – figures, reviewing and editing; Shelley Lang: Data collection, Writing – reviewing and editing; Kjell Nilssen: Data collection, Writing – reviewing and editing; Mike Hammill: Conceptualisation, Planning, Writing – reviewing and editing

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