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1994 Pup Production of Northwest Atlantic Harp Seals, *Phoca Groenlandica*

by

G. B. Stenson[1], M. O. Hammill[2], M. C. S. Kingsley[2], B. Sjare[1], W. G. Warren[1], and R. A. Myers[1]

[1] Department of Fisheries and Oceans, Science Branch
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

[2] Department of Fisheries and Oceans, Science Branch
P. O. Box 1000, Mont-Joli, Quebec, Canada G5H 3Z4

Abstract

The annual pup production of harp seals in the northwest Atlantic was estimated using a combination of photographic and visual surveys flown off eastern Newfoundland ('Front') and in the Gulf of St. Lawrence ('Gulf') during March 1994. Whelping seals were dispered into numerous concentrations, particularly at the Front and in the Northern Gulf. Pup production was estimated to be 446,700 (SE=57,200) at the Front, 57,600 (SE=13,700) in the northern Gulf and 198,600 (SE=24,200) in the southern Gulf (Magdalen Island). for a total of 702,900 (SE= 63,600). Photographic counts were corrected for misidentifed pups by comparing multiple readings of photographs made by two or more readers. Estimates were also corrected for pups absent from the ice at the time of the survey using distinct age-related developmental stages.

Introduction

The harp seal (*Phoca groenlandica*) is an abundant, ice-breeding phocid which migrates annually between the sub-Arctic and Arctic regions of the Atlantic. In the northwest Atlantic, harp seals whelp either in the Gulf of St. Lawrence (Gulf) or off the coast of southern Labrador and northeastern Newfoundland (Front); the largest concentration occurs at the Front (Stenson et al. 1993; Sergeant 1991).

Prior to 1990, the annual pup production of this population was investigated using a variety of techniques including survival indices, catch at age analyses, and sequential population models (Sergeant 1971, 1975; Benjaminsen and Øritsland 1975; Winters 1978; Cooke 1985), aerial photographic surveys (Lavigne et al. 1980, 1982), and mark-recapture experiments (Bowen and Sergeant 1983, 1985). Unfortunately, the results of these studies were often conflicting because of the different techniques used. For example, estimates ranged from approximately 250,000 (Lavigne et al. 1980, 1982) to 450,000-534,000 (Bowen and Sergeant 1983, 1985) for the 1975-1983 period. In a review of the various estimates, the Royal Commission on Seals and Sealing in Canada (Anon. 1986) concluded that pup production in 1978 was in the order of 300,000-350,000.

In 1990, pup production was estimated using a combination of photographic and visual aerial surveys (Stenson et al. 1993). An estimated 467,200 (SE=31,200) pups were born at the Front, 106,300 (SE=23,000) in the southern Gulf (Magdalen Islands area) and 4,373 (SE=1,264) in the northern Gulf (Mecatina) for a total of 577,900 (SE=38,800). This estimate indicated that pup production had likely increased from the early 1980's to 1990 but due to the disagreement among earlier estimates and the use of different estimation methods, the actual rate of increase could not be determined.

The objective of this study was to estimate the 1994 pup production of harp seals in the northwest Atlantic using methods directly comparable to those used in 1990. These results allow us to estimate the rate of increase in pup production in recent years.

Materials and Methods

Reconnaissance Surveys

Whelping concentrations ('patches') were located using fixed-wing and helicopter reconnaissance surveys of areas historically used by harp seals. At the Front and in the northern Gulf of St. Lawrence, fixed-wing reconnaissance flights were conducted during 6 - 23 March (Fig. 1). Repeated systematic east-west transects, spaced 18.5 km apart, were flown at an altitude of 230 m from the coastal edge of the ice pack to the seaward edge between 48°N and 54°20'N at the Front and between 50°50'N and 47°58'N in the northern Gulf. Satellite and VHF radio transmitters were deployed in major whelping concentrations to facilitate relocation and monitor ice movements.

In the Gulf, reconnaissance flights were flown 1-7 March using helicopters and fixed wing aircraft (Fig. 2). Helicopter flights were concentrated to the northwest of the Magdalen Islands. North-south transects spaced approximately 11 km apart were flown at an altitude of 305 m, between 63°'W and 64°'W to the west of the Magdalen Islands and 60° and 61°40' W to the east of the Magdalen Islands using fixed-wing aircraft. The northern edge of each transect was determined by the availablility of suitable ice. The area to the south of Magdalen Islands, between 46°32'N - 46°40'N and 62°34 - 62°43'W, was examined on 13 March while searching for whelping hooded seals (*Cystophora cristata*).

Photographic Surveys

Fixed-wing aerial photographic surveys were flown using two planes equipped with 23 x 23 cm format metric mapping cameras (Zeiss RMK/A) with a motion compensation mechanism. One plane, fitted with a camera using a 150 mm (6 in) Sonnar lens, flew at altitudes of 153 and 185 m (500 and 600 ft),depending upon weather conditions. The second plane flew at altitudes of 305 and 370 m (1000 and 1200 ft) and used a camera with a 300 mm (12 in) lens, thereby obtaining the same coverage per photograph. Images covered areas of 229 X 229 m and 276 X 276 m per photo for surveys at 153/305 m and 185/370 m altitudes respectively. There was overlap between consecutive frames for the photographic plane flying at the higher altitudes. At the lower altitudes frames were non overlapping with coverage varying between 60 - 80% along a transect. The camera was turned off when no seals were observed along a transect line. Correct altitude and transect spacing was maintained using barometric altimeters and GPS navigation systems. AGFA PAN 200 aerographic black-and-white film was used for all surveys.

At the Front, surveys were carried out between 14 - 21 March. The survey in the southern Gulf was flown 9 March. Surveys in the northern Gulf were conducted on 22 and 23 March. Transect spcing was chosen to ensure that the pre-defined area was completely surveyed in a single day. If sufficient fuel was available, additional transects were flown between previously flown transects. Ice drift was monitored by satellite transmitters to ensure that transects remained independent.

All surveys were based on a systematic sampling design with a single random start. The sampling unit was a transect of variable length. The estimate of the number of pups for each survey region was the sum of pups on the photographs over all transects, correcting for non-contiguous photographs and the transect spacing. The data were analyzed using the methods outlined in Hammill et al. (1992), and Stenson et al (1993, 1994).

Groups of adjacent transects were defined based on homogeneous transect spacing. For each group a weighting factor k_i was calculated as

$$k_i = S_i/W_i \tag{1}$$

where:
S_i = transect spacing (km) for the i^{th} group;
W_i = transect width (km) for the i^{th} group.

The number of pups present were summed over transects (x_j). For photographic surveys where frames did not overlap

$$x_j = \frac{\sum_{z=1}^{f_j} t_{jz} l_j}{f_j p_j} \tag{2}$$

where:
f_j = the number of photographs on transect line j ;
t_{jz} = the number of seals in the z^{th} frame on the j^{th} transect ;
l_j = the total transect length ;
p_j = the frame length ;

The estimated number of pups for the i^{th} survey is given by

$$\hat{N}_i = k_i \sum_{j=1}^{J_i} x_j \tag{3}$$

where:
J_i = *the number of transects in the* i^{th} survey ;

The estimates of error variance were based on serial difference between transects (Cochran 1977 p. 225; Kingsley et al. 1985) calculated as

$$V_i = \frac{k_i(k_i-1)J_i}{2(J_i-1)} \sum_{j=1}^{J_i-1} (x_j - x_{j+1})^2 \tag{4}$$

Photographs on some transects did not overlap. We assumed that the density of pups on the unobserved portions was the same as on the observed. The additional component of error that arose from this assumption contributes to the between-transect variation.

If transect spacing changed within the survey area, each area of homogeneous transect spacing was treated as a separate survey with the estimated number of pups given by

$$\hat{N}_i = k_i \left[x_{i1}/2 + \sum_{j=2}^{J_i-1} x_{ij} + x_{iJ_i}/2 \right] \tag{5}$$

where:
J_i = the number of transects in the i^{th} group ;
x_{ij} = the number of pups counted on the j^{th} transect in the i^{th} group.
and the end transects are the limits of the survey area.

The variance estimate was given by

$$V_i = \frac{k_i(k_i-1)}{2} \sum_{j=1}^{J_i-1} (x_j - x_{j+1})^2 \tag{6}$$

The combined estimate for total population and its error variance for the entire population are obtained by

$$\hat{N} = \sum_{i=1}^{I} N_i \tag{7}$$

$$\hat{V} = \sum_{i=1}^{I} V_i \tag{8}$$

where I is the number of groups of transects.

Positive prints were examined by five readers. Each frame was examined using an illuminated hand-lens (7-8X mag.) or a rail-mounted low magnification binocular microscope. To standardize the readers, each examined selected frames and compared seals identified. Once the cues used to identify seals were consistent among readers, all photos were read once. For each photograph the number and position of all pups were recorded on either a clear acetate overlay or a coding sheet.

After all photographs were read, four of the readers reread a series of their photographs in sequence to determine if identifications had improved over the course of the readings. Differences between first and second readings were observed for one of the Gulf readers (Reader 4). To develop a correction factor for improvements in readings ('learning curve'), this reader reread the first 276 photographs in order and then every twentieth of the remaining images. The original readings were replaced with second readings for the first 276 photographs. Regressing the first readings on the second for the remaining photographs resulted in a correction factor of $x_2 = 1.055x_1$ where x_1 is the first count and x_2 is the second. The regression was applied to the remaining photographs to make them equivalent to the 'second' readings. These readings were used in subsequent corrections and the error associated with scatter around the regression line was incorporated in the total variance for the photograph.

To correct for misidentified pups, a series of randomly selected frames, originally examined by each of the readers, were re-examined by two or more readers. The objects identified as pups on each image by individual readers were compared to determine if they were correctly identified. Any object which could not be positively identified was not included. The corrected count was considered to be the best estimate of actual number of seals present. These counts were used to develop regressions to correct for pups missed during the original readings. For each reader, the frames on which no pups were identified were compared to the 'true' counts in order to estimate the intercept a. Constraining the intercept, the non zero counts (x) were then regressed on the 'true' counts (y), $x = a + by$ to estimate the slope b. Individual photo counts were corrected using the appropriate regression for each reader. The measurement error associated with variation about the regression was estimated, summed over transects and totaled for each strata or survey to estimate the total measurement-error for the patch. This in turn was added to the sampling variance. The regressions used to correct counts for misidentified pups are given in Table 1.

Visual Surveys

Systematic visual surveys of the major whelping concentrations were flown using either one or two helicopters at an altitude of 46 m. Observers, seated in the left and right rear seats, counted all pups within a predefined strip width. Pups partially within the strip along the lower boundary were included in the survey while those along the upper boundary were not. An average survey width of 32.5 m on each side of the aircraft was used at the Front while a strip 35 m wide was counted in the Gulf. Following the surveys, the viewing areas were checked to ensure accurate strip widths during surveys. Each transect began when a navigator, seated in the front, encountered seals and was terminated approximately 5 km after the last seal was observed. The survey ended when no seals were seen on transect and were not observed outside of the survey area. Visual surveys were carried out between 13 - 19 March at the Front and 7 -12 March in the southern Gulf. The analysis methods used were the same as those used for the photographic surveys, assuming complete coverage along a transect.

Correcting for the Temporal Distribution of Births

Throughout the survey period, pups were classified into 7 distinct age-dependent stages based on pelage and morphometric features (Stewart and Lavigne 1980). Classifications were standardized among observers prior to the survey to ensure consistency. On each day, as series of random points were chosen along transverse flight lines flown across the long axis of the patch. At each locatión observers classified the first 20-30 pups encountered.

Given information on the proportion of pups in each of these developmental stages several days apart and the duration of each stage, it was possible to estimate the distribution of births over the pupping season. This information was used to correct an aerial survey estimate of abundance for those pups that have yet to be born at the time of the survey (Bowen et al. 1987; Myers and Bowen 1989, Stenson et al. 1993). A summary of the methods used to model the stage transitions are given below; see Myers and Bowen (1989) for details.

Developmental stages are denoted by the subscript j, and a pup passes from stage j to $j+1$. Stage duration are specified in terms of instantaneous transition intensity functions: $\phi_j(\tau) = \lim_{\Delta\tau \to 0}$ (probability an animal passes from stage j to $j+1$ in the interval $[\tau, \tau + \Delta\tau])/\Delta\tau)$, where τ is the time spent in stage j. This specifies the force of transition into stage $j+1$ from stage j, given that the animal has spent time τ in stage j. Note that the transition intensities depend only on the current stage and the time already spent in that stage. The rate at which pups enter stage j at time t is denoted by $m_j(t)$, and is given by the recurrence relationship:

$$m_j(t) = \int_0^\infty m_{j-1}(t-\tau)\phi_{j-1}(\tau)\, d\tau. \qquad (9)$$

If there is no mortality, the total number of pups in stage j that can be observed at time t, $n_j(t)$, is the integral of the rate pups entered stage j time τ ago times the probability that those pups have not entered stage $j+1$, i.e.

$$n_j(t) = \int_0^\infty m_j(t-\tau)\left(1 - \int_0^\tau \phi_j(s)\, ds\right)\, d\tau \qquad (10)$$

Equations (9) and (10) adequately describe stages 1-5. By stage 6 a substantial fraction of pups have left the ice and entered the water and therefore, the fraction of stage 6 pups that are not visible must also be estimated.

The transition intensity, ϕ_j, of stages 1, 2, 3, and 4 was assumed to follow a gamma density. That is, $\phi_j(t) = \rho_j(\rho_j t)^{\kappa_j - 1} e^{-\rho_j t}/\Gamma(\kappa_j)$ where κ_j is the shape parameter, ρ_j is the scale parameter, and $\Gamma()$ is the gamma function. The parameters used were estimated in Myers and Bowen (1989).

Four parameters are required to describe the model: three to specify the location and shape of the probability distribution of births over time, $m_1(t)$, and one to describe the fraction of stage 6 pups that are visible. They are estimated using a maximum likelihood method described in Myers and Bowen (1989). The model output provides an estimate of the fraction of the total pups born that are visible to be photographed on any day.

Results

Reconnaissance Surveys

A large whelping concentration (N1) was located off Labrador between 53°36'N 55°5'W and 53°39'N 55°3619'W while a series of smaller concentrations (N2-4) were identified to the southeast (Fig. 3). A second large concentration (S1) was located between 50°20'N 50°23'W and 49°50'N 50°50'W. The area between N4 and S1, denoted as S2, contained small, scattered concentrations of whelping seals. During the survey period the northern concentrations dirfted southward whiel the southern concentrations remained relatively stable (Fig. 4). All of the concentrations remained distinct and could be identified throughout the survey period.

Two areas containing scattered groups of harp seals (NG1, NG2) were identified in the northern Gulf (Fig.3). In the southern Gulf concentrations of whelping seals were located 70 km NNW of the Magdalen Islands between approximately 47°30' N and 48°20' N and 60°50'W and 62°50'W (Fig. 3). A second, small concentration was located east of the Islands between 47°10'N and 47°40'N and 60°00'W to 61°30' W.

Photographic Surveys

The four northern whelping concentrations were surveyed on 14 March at an altitude of 185 m. A series of 12 transects were flown between 51°52'N and 53°8'N (Fig. 5). Transect spacing for the three smaller concentrations (N2-4) was 14.8 km (n=6) while the largest concentration (N1) was surveyed in two strata with transects spaced 7.4 km (n=4) and 14.8 km (n=2) apart respectively. Pup production in N1, uncorrected for the temporal distribution of births, was estimated to be 269,100 (SE=115,500; Table 2). Patches N2-4 were estimated to contain 7,400 (SE=2,900), 38,100 (SE=2,000) and 15,300 (SE=14,600) respectively .

Improved coverage of concentrations N1 and N2 was obtained on 16 March. Nine (9) transects spaced 1.8 km apart and six (6) spaced 3.6 km apart were flown over N1 while seven (7) transects at intervals of 3.6 km were flown over N2. All surveys were conducted at an altitude of 185 m (or equivalent). An estimated 197,400 (SE=42,300) pups were present in N1 while 10,900 (SE=2,200) were in N2 (Table 2).

The S1 whelping concentration was surveyed on 20 and 21 March. The first survey consisted of eight (8) transects, flown at an altitude of 153 m, with transects spaced at 7.4 km intervals. This resulted in a estimate of 95,600 (SE=20,000) pups (Table 2). On 21 March, six (6) transects, spaced at 11.1 km intervals, were flown at an altitude of 185 m. An estimated 122,500 (SE=60,300) pups were present (Table 2).

The area between 50°50'N and 51°30'N (S2) was surveyed on 21 March. A number of small, scattered whelping concentrations were located but could not be surveyed independently. The area between 51°12'N and 51°30'N was surveyed at 11.1 km intervals (n=4) while three (3) transects, between 50°50'N and 51°12'N, were spaced 18.5 km apart. All surveys were flown at the equivalent of 153 m. Pup production in this area was estimated to be 102,400 (SE=52,200; Table 2).

In the northern Gulf, seven (7) transects were flown between 49°58'N and 50°06'N (NG1) and 13 transects flown between 50°32'N and 50°55'N (NG2) on 22 and 23 March respectively. Surveys were flown at an altitude of 185 m and transects were spaced at intervals of 3.6 km. An estimated 26,100 (SE=5,700) and 31,500 (SE=12,500) pups were present in NG1 and NG2 respectively (Table 2).

The main southern Gulf whelping concentration (SG1) was surveyed 9 March at an altitude of 185 m (or equivalent). A total of 28 transects divided into 9 strata with transect intervals of 1.3, 25, 5, 2.5, 5, 2.5, 7.6, 12.6, and 2.5 km apart respectively, were flown (Fig. 6). Pup production was estimated to be 160,000 (SE=24,000; Table 2).

The highest densities of pups present along transect lines occurred in N1; densities ranged from 118.0 - 556.6 pups/km^2 (mean = 206.6 pups/km^2) on 14 March and over 1700 pups/km^2 (mean = 280.0 pups/km^2) on 16 March. Average densities were much lower in the other concentrations at the Front and in the northern Gulf, ranging from 15.4 pups/km^2 in N2 to 44.7 pups/km^2 in S1. In the southern Gulf, densities ranged from 15.6-383.8 pups/km^2 in the main patch (mean = 101.5 pups/km^2)

Visual Surveys

Pup production in five whelping concentrations at the Front (N1, N2, N3, S1, S3) were also estimated using visual surveys. Surveys of N1 and N2 were conducted on March 14; pup production in N1 was estimated based on 31 transects while 16 transects were flown over N2. Transects were spaced at 1.85 km intervals for both surveys. Pup production in N1, estimated to be 129,600 (SE=13,400), was lower than that estimated by the photographic surveys for the same area (Table 2). The methods used to reconcile the apparent discrepancy is presented in Appendix 1. The estimate for N2, 7,500 (SE=2,100), is similar to that obtained from the photographic surveys.

N3 was surveyed on 13 March. A total of 13 transects, spaced 1.85 km apart, resulted in an estimate of 13,600 (SE=2,600; Table 2). Comparing the area surveyed with reconnaissance flights and photographic surveys indicates that the survey coverage was incomplete with significant numbers of pups present to the west of the survey area.

Surveys of S1 were carried out on 19 and 20 March. Twenty-four transects, consisting of two small strata with transect intervals of 3.7 km (n=3 for each) separated by a third strata with transects (n=18) spaced 1.85 km apart, were flown on 19 March. An additional seven (7) transects, 1.85 km apart, were flown on 20 March to survey two small groups located adjacent to the main concentration. A total of 137,700 (SE=17,700) pups were estimated to be present (Table 2).

In the southern Gulf, the main whelping concentration (SG1) was surveyed with a total of 15 transects divided into 5 strata. The majority of the concentration was surveyed on 9 March with some outlying groups surveyed on 12 March. Transect spacing was 3.8, 7.6, 3.8, 7.6, and 3.8 km apart (Fig. 7). A few small whelping groups located to the west of the main concentration were not surveyed visually but were included in the photographic surveys. Pup production was estimated to be 157,700 (SE=43,400; Table 2). Twenty-seven (27) transects, divided into 8 strata, were flown on 7 March during the survey of SG2 (Fig. 7). Transect spacing was 3.8, 7.6, 3.8, 7.6, 3.8, 7.6, 3.8, 7.6 km apart. Pup production was estimated to be 15,000 (SE=3,300; Table 2).

The density of pups along a transect averaged 112.6 pups/km^2 (range 3.0 - 303.2 pups/km^2) and 22.4 pups/km^2 (2.5 - 81.9 pups/km^2) in concentrations N1 and N2 respectively. In N3, densities varied from 4.5 pups/km^2 to

246.4 pups/km^2 with an average of 69.9 pups/km^2. Densities of pups varied between 4.0 and 254.6 pups/km^2 (mean = 71.6 pups/km^2) in S1. In the southern Gulf, mean densities were 27.4 pups/km^2 (*range* = *0.4-96 pups/km*^{2}) and 10.6 pups/km^2 (range = 0.5-52.8 pups/km^2) seals/km^2 for SG1 and SG2 respectively

Corrections for the Temporal Distribution of Births

Estimates of the proportion of pups in the each developmental stage were obtained from four whelping concentrations at the Front (N1, N2, N3, S1; Table 3) and both concentrations (SG1, SG2) in the southern Gulf (Table 4).

The corrections applied to the various whelping concentrations and the estimated date of first pupping are summarized in Table 5. A Weibull distribution *function* was applied to all of the stage data and model fits were good. With few exceptions, the estimated proportion of pups present at the time of the survey were high (> 90%) and therefore, little correction was necessary.

The two days of staging available for N2 were not sufficient to estimate the birthing ogive. Although the data available indicates that significant numbers of pups were born after the survey was carried out (14 March), the correction for N1 was applied to the results. This correction is more conservative than that applied to N3, which may have also been used. Considering the small number of pups present in this concentration, the use of a different correction factor would not make a significant difference.

No stage determinations were obtained from N4, S2 or the northern Gulf whelping concentrations. Given the close proximity of S1 and S2 and the similarity of pup sizes observed on the photographs, the small correction (95.7% present) estimated for S1 was applied to S2. No correction was applied to the remaining concentrations. However, it is likely that only a small correction would be necessary for the northern Gulf which was surveyed on 22 and 23 March. The pups identified on the photographs were large and, given the data available for the other concentrations, most pupping had likely occurred.

Estimated Pup Production

The estimates of pups born in each of the whelping concentrations at the Front, corrected for the temporal distribution of births, are shown in Table 6. *If more than one* estimate was available for an individual concentration, the estimates were weighted using the inverse of the variances and averaged. Combined estimates were not calculated for concentrations N3 and SG1 as the visual estimates were considered to have been incomplete.

Combining the averaged results for three concentrations (N1, N2, S1) and using the single estimates for the remaining three (N3, N4, S2) results in a total estimate of pup production at the Front of 446,700 (SE=57,200) pups. An additional 198,600 (SE=24,200) were born in the southern Gulf (SG1, SG2) and 57,600 (SE=13,700) in the northern Gulf (NG1, NG2). Therefore, the total pup production of harp seals in the northwest Atlantic was estimated to be 702,900 (SE=63,600).

Discussion

Whenever possible, the estimate for pup production in the whelping concentrations was determined by averaging multiple estimates. For three of the areas (N1, N2, S1) we had three independent estimates, two photographic and a visual. The visual and photographic estimates of N2 conducted on the same day were almost identical while the estimate made two days later was only slightly larger. Although the surveys of S1 were conducted on different days, we were able to compare the transect lines for each survey by correcting for ice drift based on the movements of a satellite transmitter located just north of this concentration. *The visual survey appeared* to have included an area to the north of either photographic survey which may account for the larger estimate obtained from the visual survey. However, given the uncertainty associated with estimating ice drift, we felt that it would be best to assume that they covered the same area and average the estimates.

Although the differences are not statistically significant, the visual survey estimate for N1 was lower than either of the photographic estimates. The high densities of pups encountered during the visual surveys may have resulted in undercouning due to observer saturation but this does not appear likely. The observers did not note any difficulties in maintaining their counts, no differences in counts were observed among observers, and similarly high densities were surveyed in 1990 by many of the same observers (Stenson et al. 1990) Comparing the empirical cumulative distributions of non zero counts for the photographic and visual transects obtained on 14 March showed strong resemblences in the two data sets (Appendix 1). Even though it was not possible to match each transect in the two surveys precisely, and it was evident that seals were not distributed evenly thoughut the concentration, the similarities between the two data sets were consistent when ice drift was taken into account. Thus, there was not reason to doubt either of the surveys and both estimates appear to be valid.

Two estimates were available for N3 and SG1 but in both cases, the coverage obtained during the visual surveys were incomplete and the photographic surveys were used. Comparing the N3 survey lines flown on 13 March (visual) and 14 March (photographic) and correcting for ice drift, indicates that the photographic transects extended much further west than the visual transects. Since these photographs contained a number of pups, the visual survey was considered to be an underestimate. In the southern Gulf (SG1), a small group of seals located to the west of the main patch were included in the photographic survey but not in the visual. If we assume, however, that pup production in this group was small, there is a good agreement between the visual and photographic surveys of the main concentration.

Generally, the corrections required for misidentified pups on the photographs were less than those used in the 1990 survey (Stenson et al. 1993). The variance around the regressions lines were low and did not appear to increase with numbers of pups present. Flying at lower altitudes and the use of a motion compensation mechanism provided larger, sharper images that were easier to identify. Usually, pups were identified by their body shape although flippers were often recognized. All but one of the readers (reader 1) were inexperienced prior to this survey. However, all but one reader were able to spend sufficent time training prior to beginning their counts or reread their photos once they had finished, to ensure that their counts were as accurate as possible.

In this survey, the 'true' estimate of the number of pups present on a photograph was determined by comparing multiple readings of the same photograph by two or more readers. This method appeared to result in good estimates of the actual numbers of pups on a photograph and additional readings did not result in any changes. In the 1990 survey, the 'true' numbers of pups present on the test photographs were estimated by comparing ultra-violet and black and white images of identical areas (Stenson et al. 1993). The use of an ultra-violet camera system increased the visibility of white-coated pups by providing a dark pup image against a white background (Lavigne 1976). This was necessary due to the small images obtained during the 1990 survey which was flown at an altitude of 305 m (using a camera system with a 150 mm lens) resulting in images 50% smaller than those obtained during this survey. The large image sizes made it unecessary to use an ultra-violet camera. Ni et al. (1988) found that identical numbers of pups were present on test transects obtained concurrently using an ultra-violet and black and white camera system with the lens size/altitude combinations flown during the current survey. The use of finer grain film than used by Ni et al. (200 ASA vs 320 ASA) and a motion compensation mechanism further reduce the possibilty that additional pups may have been identified by using ultra-violet images. By not using the ultra-violet camera, we avoided a number of problems such as the need for specialized equipment which is difficult to obtain, the limited coverage, the small image size, and missidentification of ice formations or water for pups, which occurred during the earlier survey (Stenson et al. 1993).

The whelping concentrations off Newfoundland appeared to be more widely distributed than previously reported. Historically, whelping was reported to occur mainly in a few large groups at the Front (Curran and Lett 1977, Sergeant 1991, Stenson et al. 1993). In 1994, however, numerous small concentrations were found along a line between the two large concentrations (N1 and S1) and in the northern Gulf. It is difficult to ensure complete coverage when whelping is spread over such a large area, especially for the visual surveys. However, the extensive photographic transects on the Front and in the northern Gulf resulted in good coverage of these areas.

This estimate of pup production is directly comparable to the 1990 estimate of 578,000 (SE=38,000; Stenson et al. 1993; Fig. 8). Both surveys used a combination of visual and photographic surveys, corrected for reader errors and the temporal distribution of births. The 1994 estimate was significantly higher than 1990. Although different techniques were used, estimated pup production in 1994 was also significantly greater than estimates from the late 1970's or early 1980's based on either the mark-recapture experiments (Bowen and Sergeant 1983, 1985) or age composition data (Benjaminsen and Øritsland 1975; Winters 1978; Cooke 1985). Lavigne et al. (1980,1982) estimated that pup production in the mid 1970s was even lower (approximatley 250,000) but this figure cannot be compared to other estimates since all areas were not surveyed in the same year.

Pup production at the Front was lower in 1994 (446,700 SE=57,200) than in 1990 (467,000 SE=31,000; Stenson et al. 1993), but the difference was not statistically significant. In the northern Gulf, however, pup production rose from less than 1% of the total in 1990 (4,400 SE=1,300) to 7.5% (57,600 SE=13,700). The difference observed in the Front estimates between the two suveys may be due to the movement of animals between the Front and northern Gulf. Sergeant (1991) reports that whelping concentrations may not form in the northern Gulf ('Mecatina') in some years but that substantial numbers of pups (20,000 - 35,000) may be born there in others. The greatest increase in pup production was in the proportion born in the Gulf of St. Lawrence. Pup production in the southern Gulf increased from 18% of the total in 1990 (106,000 SE=23,000) to almost 26% in 1994 (200,000 SE=24,200). Winters (1978) estimated that the proportion of the total annual pup production which occurred in the Gulf from 1965 -1977 varied between 51% and 13%. We do not know why females appear to move extensively among whelping areas, but changing prey availablility or ice conditions may be a factor.

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Table 1. Regression equations used to correct for misidentified pups on photographs. Standard errors are shown in parenthesis.

Reader	N	Intercept	Slope
1	157	0.0625 (0.062)	1.071 (0.0093)
2	127	0.2 (0.1)	1.084 (0.0090)
3	30	0.6 (0.346)	1.087 (0.0342)
4	70	1.0 (0.316)	0.988 (0.0203)
5	57	1.7619 (0.290)	1.352 (0.0521)

Table 2. Photographic and visual estimates of pup production (,000's) in the northwest Atlantic during March 1994. All estimates are uncorrected for the temporal distribution of births. Standard errors are included in parenthesis.

	Photographs				Visuals	
Area	Date	Estimate	Date	Estimate	Date	Estimate
Front:						
N1	14	269.1 (115.5)	16	197.4 (42.3)	14	129.6 (13.4)
N2	14	7.4 (2.9)	16	10.9 (2.2)	14	7.5 (2.1)
N3	14	38.1 (2.0)			13	13.6 (2.6)[2]
N4	14	15.3 (14.6)				
S1	20	95.6 (20.0)	21	122.5 (60.3)	19	137.7 (17.7)
S2[1]			21	102.4 (52.2)		
Northern Gulf:						
NG1	22	26.1 (5.7)				
NG2	23	31.5 (12.5)				
Southern Gulf:						
SG1	9	160.0 (24.0)			10	157.7 (43.4)[2]
SG2					7	15.0 (3.3)

[1] Includes a number of small, scattered concentrations.
[2] Incomplete coverage.

Table 3. Numbers of harp seal pups in individual age dependent stages at the Front during March 1994.

Date	Patch	Stage							Total
		1	2	3	4	5	6	7	
Mar 8	N1	3	22	0	0	0	0	0	25
10		8	30	24	0	0	0	0	62
11		4	15	372	6	0	0	0	397
12		0	4	44	6	0	0	0	54
13		9	67	601	54	0	0	0	731
15		0	0	308	214	19	0	0	541
25		0	0	1	4	53	17	1	76
Mar 8	N3	8	6	136	5	0	0	0	155
10		0	7	95	42	11	0	0	153
11		0	2	83	7	0	0	0	92
12		1	3	58	35	0	0	0	97
15		1	0	45	47	28	0	0	121
25		0	0	0	9	4	21	2	72
Mar 13	N2	3	5	79	34	1	0	0	122
15		5	15	112	64	35	0	0	231
Mar 20	S	0	0	14	218	490	28	0	750
22		0	0	2	142	226	40	4	414
25		0	0	1	56	304	326	31	718

Table 4. Numbers of harp seal pups in individual age dependent stages in the Gulf during March 1994.

Date	Patch	Stage							Total
		1	2	3	4	5	6	7	
Feb 28	SG1	5	6	8	0	0	0	0	19
Mar 1		26	73	102	0	0	0	0	201
2		9	102	189	0	0	0	0	300
5		4	18	114	14	0	0	0	150
6		33	91	395	196	0	0	0	715
9		1	0	6	34	14	0	0	55
10		1	10	22	68	47	0	0	148
12		0	0	23	80	2	0	0	105
15		0	0	4	55	94	7	0	160
16		0	0	0	9	12	0	0	21
Mar 7	SG2	5	7	29	127	0	0	0	168
9		0	0	3	86	20	0	0	109
13		0	4	5	51	123	4	0	187

Table 5. Corrections applied for the temporal distribution of births. All models fit with a Weibull distribution.

Area	Date of 1st Pupping	Survey Date (March)	Proportion of Pups Present
N1	March 4	14	0.922
		16	0.972
N3	March 3	13	0.811
		14	0.856
S1,2	March 8	19	0.927
		20	0.944
		21	0.957
SG1	February 27	9	0.879
		10	0.918
SG2	February 28	7	0.903

Table 6. Photographic and visual estimates of pup production (,000's) in the northwest Atlantic during March 1994, corrected for the temporal distribution of births. Standard errors are included in brackets. Estimates used in the total are shown in bold.

	Photographs				Visuals		Combined
Area	Date	Estimate	Date	Estimate	Date	Estimate	Estimate
Front:							
N1	14	291.9 (115.2)	16	203.1 (42.3)	14	140.6 (13.4)	**148.1 (12.7)**
N2	14	8.0 (2.9)	16	11.2 (2.2)	14	8.1 (2.1)	**9.2 (1.3)**
N3	14	**44.5 (2.0)**			13	16.8 (2.6)[3]	
N4[1]	14	**15.3 (14.6)**					
S1	20	101.3 (20.0)	21	128.0 (60.3)	19	148.5 (17.7)	**122.6 (12.9)**
S2[2]			21	**107.0 (52.2)**			
Northern Gulf:							
NG1[1,2]	22	**26.1 (5.7)**					
NG2[1,2]	23	**31.5 (12.5)**					
Southern Gulf:							
SG1	9	**182.0 (24.0)**			10	171.8 (43.4)[3]	
SG2					7	**16.6 (3.3)**	

[1] No correction applied.
[2] Includes a number of small, scattered concentrations.
[3] Incomplete coverage.

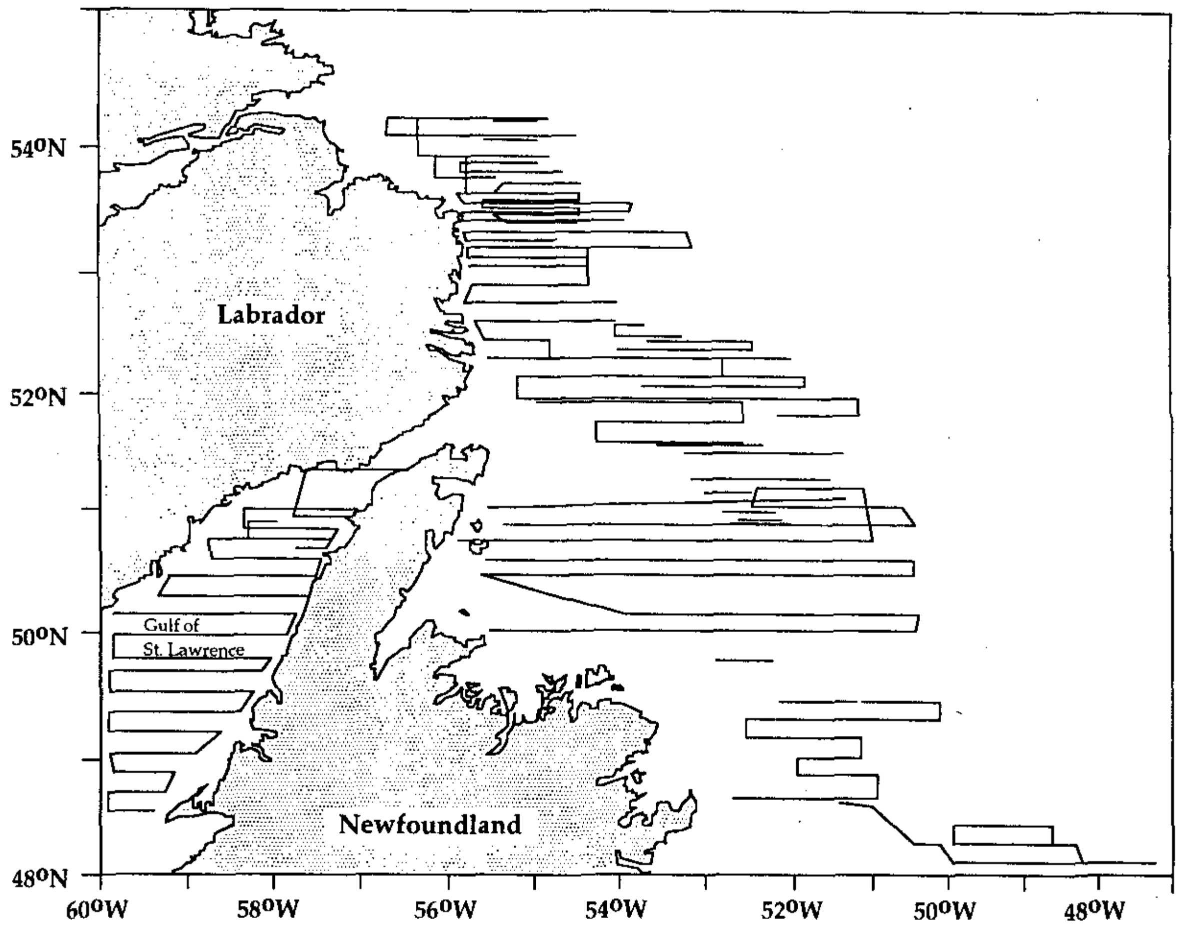

Figure 1. Aerial reconnaissance surveys conducted off Newfoundland and in the northern Gulf of St. Lawrence, 6 - 23 March 1994. Additional reconnaissance was conducted during the photographic surveys.

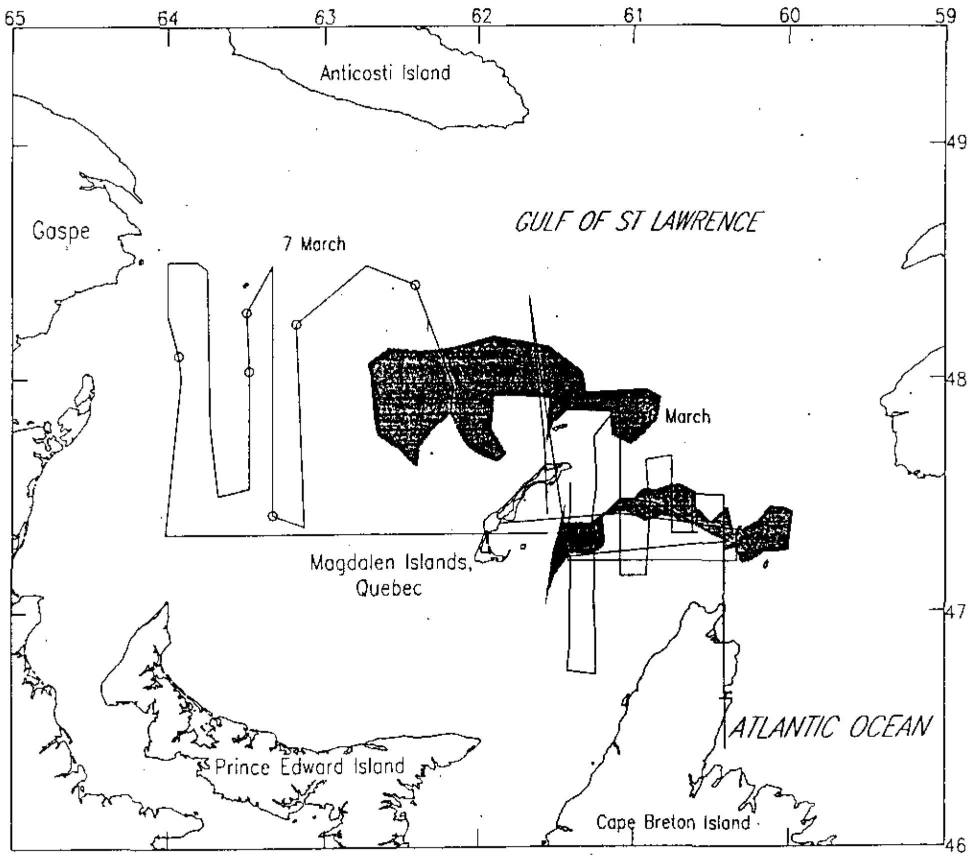

Figure 2. Aerial reconnaissance surveys conducted in the southern Gulf of St. Lawrence, 1 - 7 March 1994. Areas surveyed using helicopters are indicated by hatching; fixed-wing transects are plotted. Additional reconnaissance was made during photographic surveys.

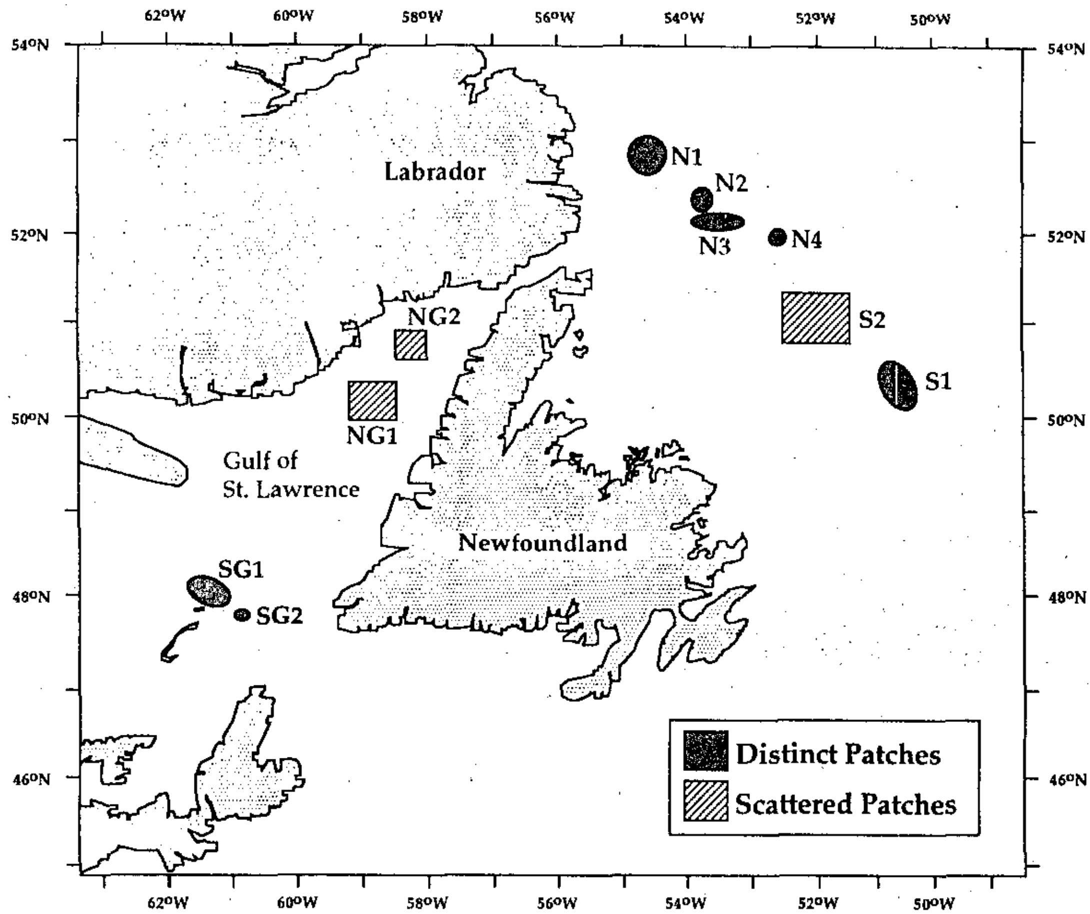

Figure 3. Locations of harp seal whelping concentrations off Newfoundland and in the Gulf of St. Lawrence during February and March 1994.

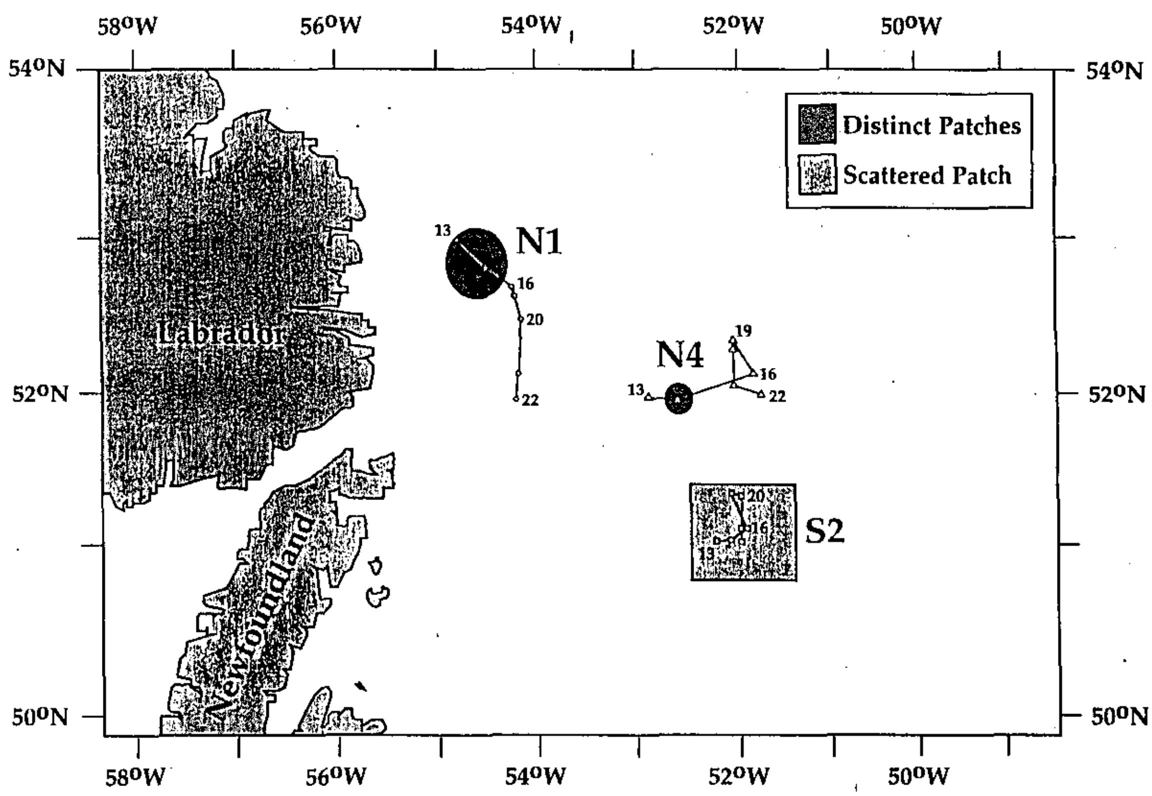

Figure 4. Movements of satellite transmitters located in distinct harp seal whelping concentrations due to drift of pack ice 13 - 22 March 1994.

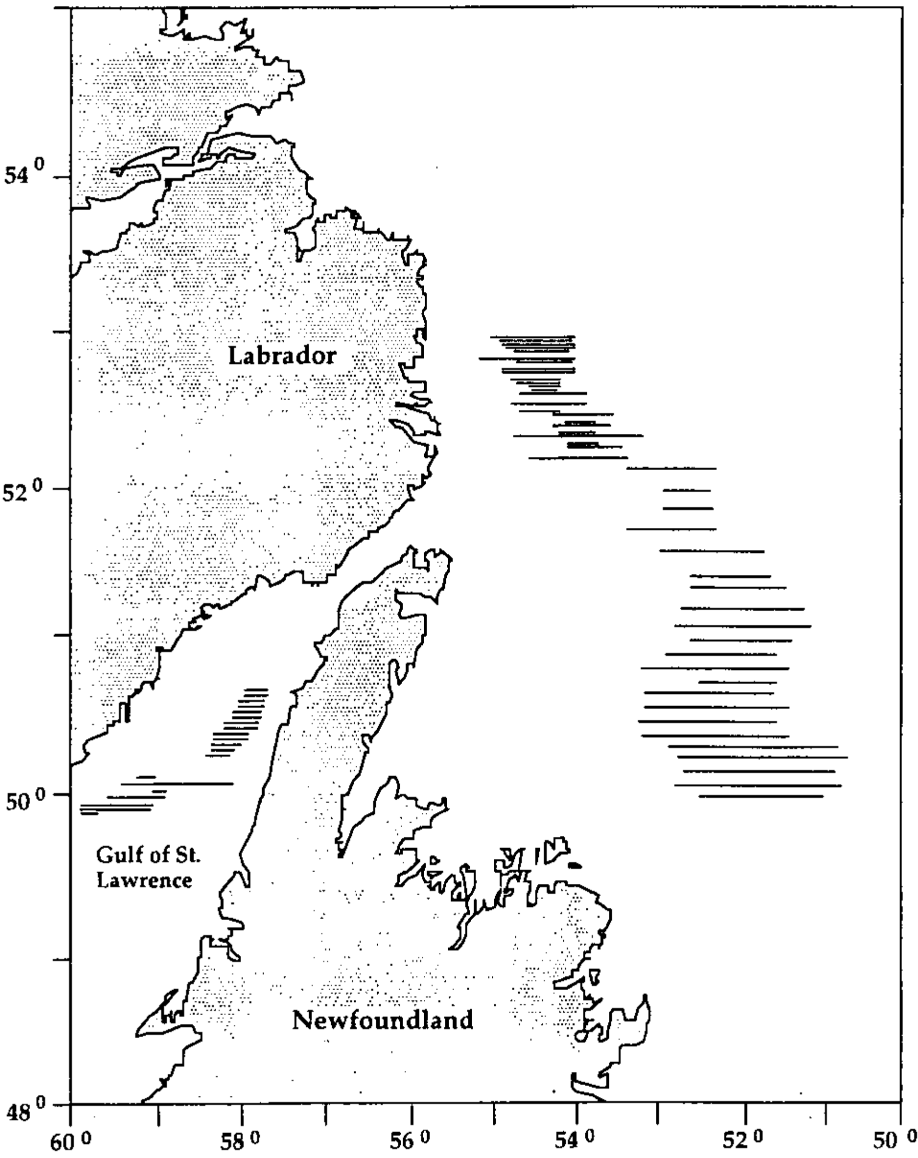

Figure 5. Photographic survey transects flown off Newfoundland and in the Gulf of St. Lawrence 14 - 23 March 1994.

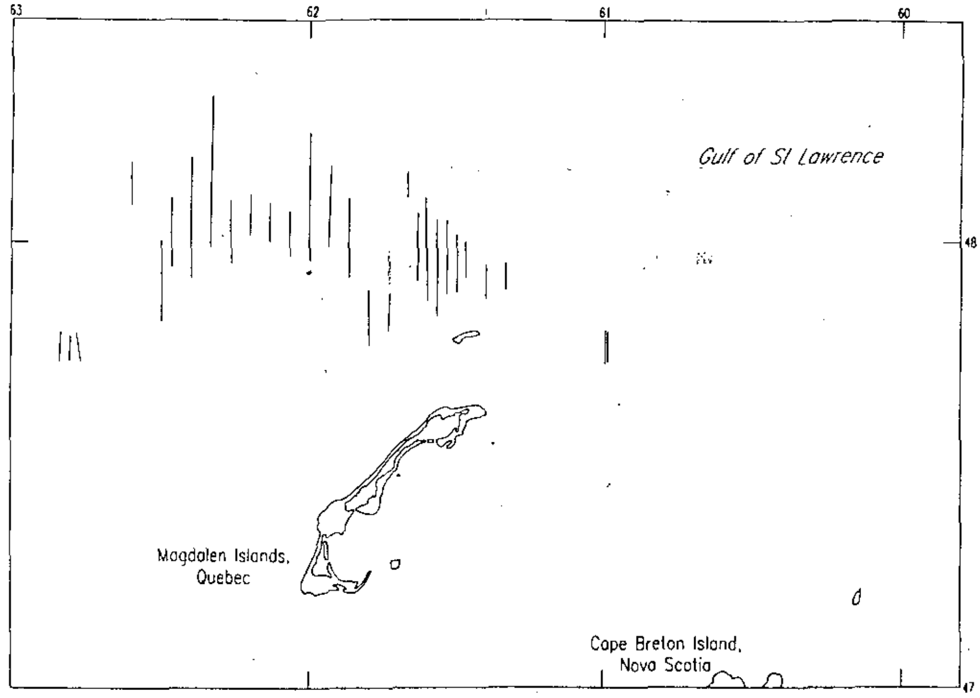

Figure 6. Photographic survey transects flown in the southern Gulf of St. Lawrence 9 March 1994.

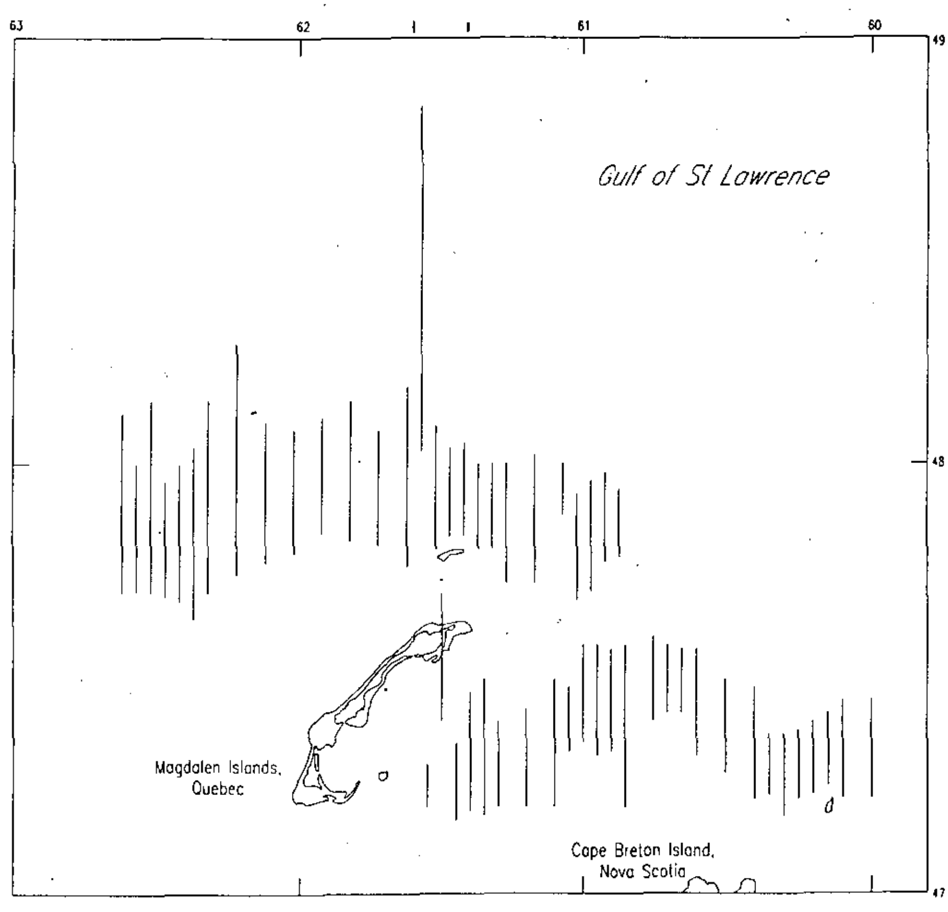

Figure 7. Visual survey transects flown in the southern Gulf of St. Lawrence 7 - 12 March 1994.

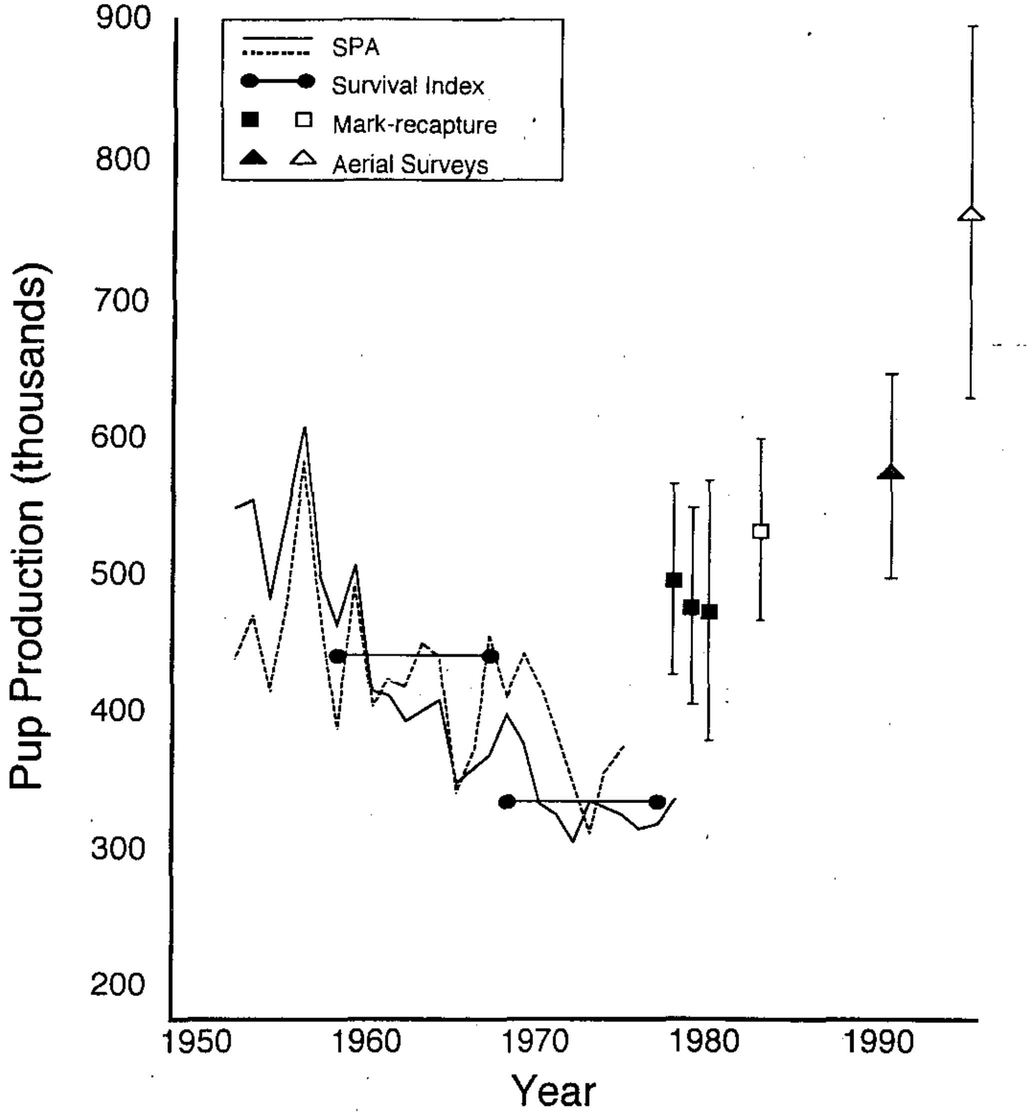

Figure 8. Estimates of northwest Atlantic harp seal pup production: cohort analysis by Winters (1978;———) and Lett and Benjaminsen (1977; --------), average production based on the survival index method of Cooke (1985) assumming moderate aging errors (●—●), mark-recapture estimates by Roff and Bowen (1986; closed box with 1SE) and Bowen and Sergeant (1983; open box with 1SE), and aerial survey estimates by Stenson et al. (1993; closed triangle with 1SE) and this paper (open triangle with 1SE).

APPENDIX 1: Reconciling the Photographic and Visual Surveys of the Northern Patch, N1.

The northen patch, N1, was visually surveyed on the morning of 14 March (31 transects), while the photographic surveys (6 transects) were carried out during the afternoon. Matching the photographic and visual transects by latitude, showed noticeably greater than expected photographic counts on all transects, except the most northerly (53°0.8′) and, perhaps, that at 53°04′.

Although the photographic transects were flown at the same latitudes as six of the visual transects, the time between the flying of a photographic transect and its "matching" visual transect varied from 1 to 6 hours. During that period the ice drifted at approximately 0.9 km/hr (based on the position of the satellite transmitter within the patch), so it is not appropriate to match photographic with visual transects exactly. Even if they could be matched by flight line, the positioning of the individual photographs along a transect is by distance, while the position of the visual counts is by time. Since (i) there was a tendency for the helicopter to slow when an aggregation of pups was encountered, (ii) the transects are of vastly different widths (so that (part of) an aggregation could appear in a photograph but be excluded from the narrower visual strip), and (iii) it is unlikely that the photographs and visuals were flown on precisely the same line (a few metres difference could well affect the visual counts), one can expect, at best, only a rough correspondence between the numbers and patterns of pups in the photographic and visual counts.

Nevertheless, the empirical cumulative distribution of the non zero counts was plotted for each photographic transect and for each visual transect (52°45′ to 53°08′). The visual counts were grouped by 10-second intervals, approximately the time taken for the visual survey to cover the distance equivalent to one photograph. This is approximate because, as noted above, the helicopter used during the visual surveys varied its speed according to the density of pups along the transect. Total counts would be unaffected but there would seemingly be a tendency to overestimate the smaller counts (since in 10 seconds the aircraft would fly further) and underestimate the larger counts. Zero counts were omitted since most occur at the ends of the transects, i.e. before the patch proper is encountered. Accordingly, it was considered more reliable to consider the cumulative distribution of non-zero counts only. For comparability the visual counts were multiplied by 4.25 (the ratio of the photographic to visual strip widths).

The emprirical cumulative distribution of the counts on each of five photgraphic transects had a strong resemblance to an empirical cumulative distribution of the counts on a visual transect within 2′ of latitude. It is difficult to find a nearby comparable match for the sixth, and most southernly, transect (52°40′) photographs but it appears that in this region the "patch" is characterized by a few widely spaced compact aggregations. In this respect, the photographic counts are consistent with the visuals from the same general area. Further, as one moves along both the photographic and visual transects near the central latitudes of the concentration, one finds either a large aggregation or aggregations in close proximity, followed by a gap and then a more compact aggregation.

Although there is a general increase in the density of the pups from the southern and northern borders to the centre of the patch, if the visual survey indicates that this is a jagged rather than a smooth progression. It is conjectured, therefore, that the discrepacy between the photographic and visual estimates of the number of pups in N1 can be attribued to differential drift of the ice. It appears that, fortuitously, 4 of the photographic transects, including the 3 more southerly and widely spaced, have roughly coincided with strips with higher pup densities than their neighbours. While one should not really think of a transects at 8 nm spacing as corresponding to concentrations 4 nm to either side, this, in effect, is what occurs in the estimation of pup totals and resulted in the larger estimate from the photographic survey. Thus, there is no reason to doubt either the visual or photographic counts; both estimates appear to be valid. However, the photographic survey carries a large standard error.