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Is there evidence of increased pup production in northwest Atlantic harp seals, *Pagophilus groenlandicus*?

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Photographic and visual surveys of the whelping (pupping) concentrations off eastern Newfoundland ("Front") and in the Gulf of St Lawrence ("Gulf") were conducted during March 1994 to determine whether pup production of Northwest Atlantic harp seals has increased since the decline in hunting during the mid-1980s and early 1990s. Photographic counts were corrected for misidentified pups by comparing multiple readings of photographs made by two or more readers. Survey estimates were also corrected for pups absent from the ice at the time of the survey using the occurrence of distinct age-related developmental stages. Multiple estimates were available for three of the ten whelping concentrations. Pup production was estimated to be 446 700 (s.e.=57 200) at the Front, 57 600 (s.e.=13 700) in the northern Gulf and 198 600 (s.e.=24 200) in the southern Gulf (Magdalen Island) for a total of 702 900 (s.e.=63 600). This result is greater than estimates obtained in the late 1970s and early 1980s using mark-recapture techniques. The 1994 estimate can be compared directly with the 1990 estimate of pup production (578 000, s.e.=38 800) which was obtained using similar aerial survey methods. The null hypothesis of no increase in pup production (one-tail t-test) was rejected (p=0.03) indicating that pup production has increased.

Keywords: pup production, abundance, harp seals, aerial surveys.

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Introduction

The harp seal (*Pagophilus groenlandicus*) is a medium-sized, ice-breeding phocid found throughout Arctic and sub-Arctic regions of the North Atlantic and adjacent areas. Harp seals are separated into three populations, the White Sea/Barents Sea, Greenland Sea, and Northwest Atlantic, based primarily upon their whelping (pupping) locations (Anon., 1994). Several studies (Yablokov and Sergeant, 1963; Meisfjord and Sundt, 1996; Perry and Terhune, 1999; Perry *et al.*, 2000) indicate that the Northwest and Northeast Atlantic populations are reproductively isolated. The largest population is found in the Northwest Atlantic, where whelping occurs on the pack ice off the coast of Newfoundland and/or southern Labrador ("Front") and in the Gulf of St Lawrence ("Gulf") from late February through March (Sergeant, 1991).

Exploited commercially since the 1700s, the harvest of Northwest Atlantic harp seals reached its maximum during the late 1800s with catches as high as 526 000 (Sergeant, 1991). Harvests declined during the early

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1900s owing to a combination of two world wars and poor economic conditions, but then increased to 350 000 animals per annum by the mid-1950s (Sergeant, 1991). These large catches continued throughout the 1950s and 1960s and by the early 1970s, pup production was thought to have been reduced by 50% from the estimated 600 000 animals born during the early 1950s (Lett and Benjaminsen, 1977; Winters, 1978). In 1971, a quota of 200 000 animals was introduced to limit the hunt in southern Canadian waters. This quota was reduced to 120 000 animals in 1972, but was later established at 186 000, a level which was lower than the estimates of replacement yield at that time (Anon., 1981). Between 1972 and 1982 catches in Canadian and Greenland waters averaged 176 600 seals per annum (Stenson *et al.*, 2000). However, between 1983 (when the European Economic Community banned the importation of the whitecoat pelts) and 1994, annual catches in southern Canadian waters declined to an average of 51 000, resulting in an average total reported harvest in all areas of 95 000 (Stenson *et al.*, 2000).

Under this reduced harvesting regime and in the absence of other major sources of mortality the harp seal population would be expected to increase. Prior to 1990, the annual pup production of this population was estimated using a variety of techniques including survival indices, catch-at-age analyses, sequential population models (Sergeant, 1971, 1975, 1991; 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). The results of these studies were often inconsistent with estimates ranging from approximately 250 000 in the mid- to late 1970s (Lavigne *et al.*, 1980, 1982) to 450 000–534 000 (Bowen and Sargeant, 1983, 1985) for the late 1970s and early 1980s. In a review of the various estimates, the Royal Commission on Seals and Sealing in Canada (Anon., 1986) highlighted the difficulties in comparing estimates obtained using different techniques, each with differing potential biases. However, they 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 (s.e. = 31 200) pups were born at the Front, 106 300 (s.e. = 23 000) in the southern Gulf (Magdalen Islands area) and 4373 (s.e. = 1264) in the northern Gulf (Mecatina) for a total of 577 900 (s.e. = 38 800). This estimate indicated that pup production had likely increased from the early 1980s to 1990, but the use of different estimation methods, each with its own potential and possibly conflicting biases, made a direct comparison among estimates difficult.

The use of photographic and visual surveys along with extensive reconnaissance and corrections for the temporal distribution of pupping, such as carried out in 1990, is considered the most appropriate method of estimating pup production in this species (Anon., 1993). The objective of this study was to estimate the 1994 pup production of harp seals in the Northwest Atlantic using methods similar to those used in 1990 to determine whether pup production has increased over this period.

Materials and methods

Identification of whelping areas

Reconnaissance surveys of areas historically used by harp seals using fixed-wing aircraft and helicopters were flown to locate whelping concentrations. Due to ice drift and a range of pupping dates (early to mid-March), most areas were surveyed repeatedly to minimise the chance of missing whelping concentrations. Satellite and VHF radio transmitters were deployed in major whelping concentrations to facilitate relocation and to monitor ice movements.

At the Front and in the northern Gulf of St Lawrence, fixed-wing reconnaissance flights were conducted 6–23 March (Figure 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.

In the southern Gulf, reconnaissance flights were flown 1–7 March using a helicopter and fixed wing aircraft (Figure 2). Repeated helicopter flights were made to the traditional early whelping area to the northwest of the Magdalen Islands. In addition, 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°W 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 availability of suitable ice. The area to the south of the Magdalen Islands, between 46°32′–46°40′N and 62°34′–62°43′W, was examined on 13 March. Ecotourism companies operating in the area also provided information on the location of seals.

Estimates of abundance

Visual surveys

The number of pups present in the whelping concentrations was estimated by conducting visual strip transect surveys (see Stenson *et al.*, 1993) from a helicopter flying at an altitude of 46 m. A navigator, seated beside the pilot, directed the survey while two observers, seated in the rear, counted all pups within a strip of 32.5 m (Front) or 35 m (Gulf) on either side of the aircraft. The strip widths were calibrated against known

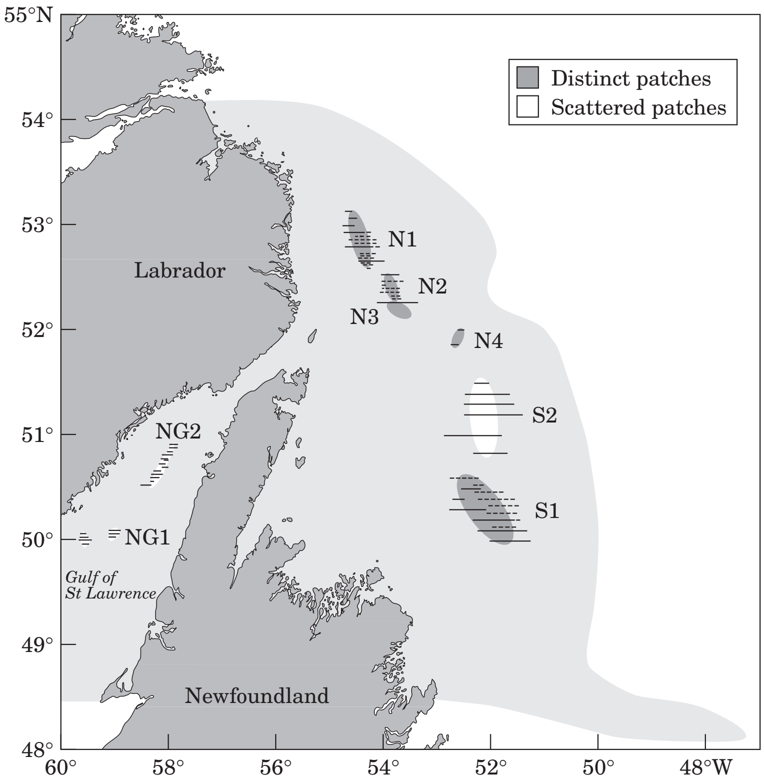

Figure 1. General locations of harp seal whelping concentrations, photographic survey transects, and areas examined for whelping harp seals (light stippling) off Newfoundland and in the northern Gulf of St Lawrence, March 1994.

distances on the ground. Visual surveys were carried out between 13–19 March at the Front and 7–12 March in the southern Gulf. No visual surveys were flown in the northern Gulf.

Photographic surveys

Fixed-wing aerial photographic surveys were flown using two planes equipped with 23 × 23 cm format metric mapping cameras (Zeiss RMK/A) with a motion compensation mechanism and AGFA PAN 200 aerographic black-and-white film. One plane, fitted with a camera using a 153 mm Sonnar lens, flew at altitudes of 153 and 185 m, depending upon cloud cover, and obtained images covering areas of 229 × 229 m or 276 × 276 m per photo at the respective altitudes. Consecutive frames were non-overlapping with coverage varying between 60–80% along a transect. The second plane used a camera with a 300 mm lens and flew at altitudes of 305 and 370 m to obtain the same coverage per photograph. The 9–13% overlap that occurred between consecutive frames was removed prior to the analysis. Both cameras were turned off when no seals were observed along a transect line. Correct altitude and transect spacing were maintained using barometric altimeters and GPS navigation systems.

Surveys were conduced between 14–21 March at the Front and on 22 and 23 March in the northern Gulf. The southern Gulf was surveyed 9 March. Transect spacing was chosen to ensure that the pre-defined area was surveyed completely 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.

Photographic counts

Positive prints were examined by five readers. Each frame was examined using an illuminated hand-lens (7–8 × magnification) or a rail-mounted binocular microscope (6–12 × magnification). Readers examined a common series of photographs 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 re-read 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

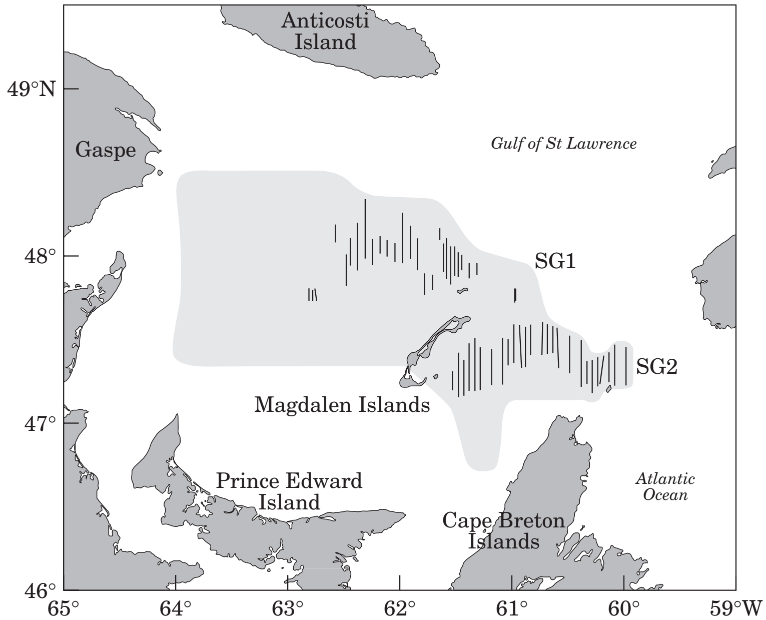

Figure 2. Locations of harp seal whelping concentrations, photographic (SG1), and visual (SG2) survey transects, and areas examined for whelping harp seals (light stippling) in the southern Gulf of St Lawrence, March 1994.

readers (Reader 4). To develop a correction factor for improvements in readings ("learning curve"), this reader re-read 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 photographic counts.

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 to determine a "best estimate" of the number of pups present. Any pup that could not be positively identified was not included. For each reader, the frames on which no pups were identified during the initial readings were compared to the "best estimate" in order to estimate the intercept "a" of a linear regression. Constraining the intercept, the non-zero counts (x) were then regressed on the "best estimate" counts (y), $x=a+by$ to estimate the slope "b". Individual photo counts were corrected using the appropriate regression for each reader (Table 1). The measurement error associated with variation about the regression was estimated, summed over transects to estimate the total measurement error for the survey, and added to the sampling variance.

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

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)

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 data were analysed using the methods outlined in Hammill *et al*. (1992) and Stenson *et al*. (1993, 1997) and summarised here.

The estimated number of pups for the ith survey is given by:

$$\hat{N}_i = K_i \sum_{j=1}^{J_i} x_i$$

where J_i=the number of transects in the ith survey; k_i=weighting factor for the ith survey determined by dividing the transect interval by the transect width; x_j=the number of pups on the jth transect.

For photographic surveys where frames did not overlap:

$$x_j = \frac{l_j \Sigma_{z=1}^{f_i} t_{jz}}{f_j p_j}$$

where f_j = the number of photographs on transect line j; t_{jz} = the number of seals in the zth frame on the jth transect; l_j = the total transect length; p_j = the frame length.

This assumes that the distribution and density of pups on the unobserved portions were similar to those in the observed. The additional component of error that arises from this assumption was judged to be small and is included in the between-transect variability.

The estimates of error variance, based on serial differences between transects (p. 225 Cochran, 1997; Kingsley *et al.*, 1985), were calculated as:

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

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:

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

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

The variance estimate was given by:

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

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

Correcting for the temporal distribution of births

To correct the estimates of abundance for pups that had left the ice or were not yet born at the time of the survey (Bowen *et al.*, 1987; Myers and Bowenm 1989; Stenson *et al.*, 1993, 1997), it was necessary to estimate the distribution of births over the pupping season. This was done using information on the proportion of pups in each of seven distinct age-dependent stages (Stewart and Lavigne, 1980) in each concentration and the duration of each stage. Prior to the survey, classifications of pup stages were standardised among observers to ensure consistency. To determine the proportion of pups in each stage on a given day, a series of random points were chosen along transverse flight lines flown across the long axis of the patch. At each location observers classified the first 20–30 pups encountered. Repeated classifications were obtained from each concentration several days apart. The methods used to model the stage transitions are given in Myers and Bowen (1989) and Stenson *et al.* (1993).

Results

Identification of whelping areas

A large whelping concentration (N1) was located off Labrador between 53°36′N 55°5′W and 53°39′N 55°19′W whereas smaller concentrations (N2–4) were identified to the southeast (Figure 1). 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. All 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 (Figure 1). In the southern Gulf a large concentration of whelping seals (SG1) was located 70 km NNW of the Magdalen Islands (Figure 2). A second, small concentration (SG2) was located east of the islands.

Visual surveys

Visual surveys were used to estimate pup production in four whelping concentrations at the Front (N1, N2, N3, S1) and two (SG1, SG2) in the southern Gulf. At the Front, N1 and N2 were surveyed on 14 March with a total of 31 and 16 transects, respectively. Transects were spaced at 1.85 km intervals for both surveys. Pup production in N1 was estimated to be 129 600 (s.e. = 13 400) while 7500 (s.e. = 2100) pups were estimated to be present in N2 (Table 2).

An incomplete survey of N3 was carried out on 13 March with a total of 13 transects spaced 1.85 km apart. Pup production was estimated to be 13 600 (s.e. = 2600; Table 2). This survey was incomplete because reconnaissance flights and photographic surveys (see below) indicated that significant numbers of pups were 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 stratum with transects (n = 18) spaced 1.85 km apart, were flown on 19 March. An additional seven transects, 1.85 km apart, were flown on 20 March to survey two small groups located adjacent to the main

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

	Photographic				Visual	
Area	Date	Estimate	Date	Estimate	Date	Estimate
Newfoundland						
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)[b]
N4	14	15.3 (14.6)				
S1	20	95.6 (20.0)	21	122.5 (60.3)	19	137.7 (17.7)
S2[a]			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)[b]
SG2					7	15.0 (3.3)

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

concentration. A total of 137 700 (s.e. = 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 27 transects divided into five strata spaced 3.8 (n=4), 7.6 (n=2), 3.8 (n=7), 7.6 (n=7), and 3.8 (n=7) km apart, respectively. The majority of the concentration was surveyed on 9 March with some outlying groups surveyed on 12 March. A few small whelping groups located to the west of the main concentration were not surveyed visually, but were included in the photographic surveys (see below). Therefore the pup production estimate of 157 700 (s.e. = 43 400; Table 2), was considered to be an underestimate. Twenty-six transects, divided into eight strata, were flown on 7 March during the survey of SG2 (Figure 2). Transect spacing was 3.8 (n=5), 7.6 (n=3), 3.8 (n=4), 7.6 (n=2), 3.8 (n=3), 7.6 (n=2), 3.8 (n=5), and 7.6 (n=2) km apart. Pup production was estimated to be 15 000 (s.e. = 3300; Table 2).

Photographic surveys

At the Front, four northern whelping concentrations were surveyed on 14 March at an altitude of 185 m with a series of 12 transects flown between 51°52′N and 53°8′N (Figure 1). 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. Patches N2-4 were estimated to contain 7400 (s.e. = 2900), 38 100 (s.e. = 2000) and 15 300 (s.e. = 14 600) pups, respectively.

Pup production in N1, uncorrected for the temporal distribution of births, was estimated to be 269 100 (s.e. = 115 500; Table 2). This estimate is substantially higher than that obtained from the visual survey on the same day, although the difference is not statistically significant ($p>0.05$), To determine if there was a reason for the discrepancy between the visual and photographic surveys of N1, both surveys were examined in greater detail. The visual survey was conducted on the morning of 14 March (31 transects spaced 1.8 km apart), while the photographic survey (six transects spaced 7.4–14.8 km apart) was flown during the afternoon. After correcting for ice drift and the difference in strip widths (multiplying the visual counts by 4.25), the cumulative distribution of the non-zero counts was plotted for each photographic and visual transect (52°45′N to 53°08′N) to determine if major differences occurred along transects. The cumulative distribution of counts on five of the six photographic transects was similar to the cumulative distribution of the counts on a visual transect within 2° of latitude. Large differences were seen between the visual and photographic surveys in the cumulative distribution of counts on the sixth line. In this region it appears that the ‘‘concentration’’ was characterised by a few widely spaced compact aggregations. Based on the much closer spaced transects obtained during the visual survey, the distribution of animals throughout the concentration appeared to be highly clumped. The fewer, widely spaced transects obtained during the photographic survey fortuitously flew over areas where larger concentrations of seals occurred, resulting in a larger estimate of pup production.

Improved coverage of concentrations N1 and N2 was obtained on 16 March. Nine transects spaced 1.8 km apart and six spaced 3.6 km apart were flown over N1 while seven transects at intervals of 3.6 km were flown

Table 3. Numbers of harp seal pups in individual age-dependent stages off Newfoundland during March 1994.

Date	Patch	Stage 1	2	3	4	5	6	7	Total
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

over N2. All surveys were conducted at an altitude of 185 m (or equivalent). An estimated 197 400 (s.e. = 42 300) pups were present in N1 while 10 900 (s.e. = 2200) were in N2 (Table 2).

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

A number of small, scattered whelping concentrations located between 50°50′N and 51°30′N (collectively referred to as S2) were surveyed on 21 March. The area between 51°12′N and 51°30′N was surveyed at 11.1 km intervals (n = 4) while three 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 resulting in an estimated pup production in this area of 102 400 (s.e. = 52 200; Table 2).

In the northern Gulf, seven 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 (s.e. = 5700) and 31 500 (s.e. = 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. A total of 28 transects divided into nine strata with transect intervals of 1.3 (n = 2), 2.5 (n = 1), 5 (n = 2), 2.5 (n = 6), 5 (n = 12), 2.5 (n = 1), 7.6 (n = 1), 12.6 (n = 1), and 2.5 (n = 2) km apart, respectively were flown (Figure 2). Pup production was estimated to be 160 000 (s.e. = 24 000; Table 2). SG2 was not surveyed photographically.

Corrections for the temporal distribution of births

Estimates of the proportion of pups in 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). A Weibull distribution was used to fit the stage data; model fits were good. With few exceptions, the estimated proportions of pups present at the time of the survey were high (>90%) and only small corrections were necessary (Table 5).

The two days of staging available for N2 were not sufficient to estimate the distribution of births. Although the data indicated that significant numbers of pups were born after the survey date (14 March), the correction for N1 was applied to the results. This correction is more conservative than that applied to N3 or an average of the two. Considering the small number of pups present in this concentration, the use of a different correction factor would not affect the overall estimate greatly.

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,

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

Date	Patch	Stage 1	2	3	4	5	6	7	Total
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 fitted 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

although it is likely that only a small adjustment would be necessary for the northern Gulf whelping areas that were surveyed on 22 and 23 March. The pups identified on the photographs were large and, given the data 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, a weighted average was calculated with weight inversely proportional to their estimated variance. 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 (s.e. = 57 200) pups. An additional 198 600 (s.e. = 24 200) were born in the southern Gulf (SG1, SG2) and 57 600 (s.e. = 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 (s.e. = 63 600). The uncertainty provided for this estimate is slightly underestimated since it does not account for the error associated with the corrections for the birth date distribution. In previous surveys this error has been in the order of 2.5–3% (Stenson *et al.*, 1993).

Discussion

The methods used in the 1994 survey are very similar to those used during the 1990 survey (Stenson *et al.*, 1993). Both used extensive reconnaissance to locate whelping seals and a combination of visual and photographic surveys to estimate pup production. Both surveys corrected the resulting estimates for errors in the reading of photographs and the temporal distribution of births. However, the two surveys differed in the way in which the "best" estimate of the number of pups present on a photograph was determined. In contrast to the 1994 survey, where multiple readings of the same photograph by two or more readers were compared, the 1990 survey photo counts were corrected by comparing ultraviolet and black and white images of identical areas (Stenson *et al.*, 1993). The use of an ultraviolet camera system, which increased the visibility of white-coated pups by providing a dark pup image against a white background (Lavigne, 1976), was necessary due to the small images obtained during the 1990 survey, which was flown at an altitude of 305 m using a camera with a 150 mm lens. The resulting images were 50% smaller than those obtained during the 1994 survey. However, comparison of images obtained from the two systems identified a problem with false positives in the ultraviolet imagery during the 1990 survey (Stenson *et al.*, 1993). Owing to

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

Area	Photographic				Visual		Combined
	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)[c]	
N4[a]	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)**
S22			21	**107.0 (52.2)**			
Northern Gulf							
NG1[a,b]	22	**26.1 (5.7)**					
NG2[a,b]	23	**31.5 (12.5)**					
Southern Gulf							
SG1	9	**182.0 (24.0)**			10	171.8 (43.4)[c]	
SG2					7	**16.6 (3.3)**	

[a]No correction applied.
[b]Includes a number of small, scattered concentrations.
[c]Incomplete coverage.

the low coverage of the ultraviolet imagery (70 mm format vs. 23 cm for black-and-white) and the potential bias associated with the images, this system was not used in 1994. This is unlikely to have resulted in biased estimates because previous studies comparing test images from an ultraviolet system and black and white camera system with the lens size/altitude combinations flown in 1994 found identical numbers of pups on the two systems (Ni *et al.*, 1988).

In 1994, we reduced the possibility of missing pups by flying at a lower altitude than in 1990, using a motion compensation mechanism on the camera and a finer grain film to improve image quality. The larger and clearer images on the 1994 photographs improved our ability to detect seal pups during the first reading and thus reduced the training readers required and the amount of correction for reader error that had to be applied to the photo counts. Also, the variances around the regressions lines to correct the reader counts were lower in 1994 and did not appear to increase with numbers of pups present, as was the case in 1990 (Stenson *et al.*, 1993). In spite of the difference in how the reader correction was obtained, the basic similarity in the 1990 and 1994 surveys allows them to be directly compared.

Using a combination of photographic and visual surveys allowed us to obtain multiple estimates of a number of whelping concentrations that could be averaged to provide a more precise estimate of pup production. Three independent estimates, two photographic and one visual were available for three of the areas (N1, N2, S1). 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 that 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 the three surveys covered the same area and to average the estimates.

The visual survey estimate for concentration N1 was much lower, although not significantly different, than those obtained from the photographic surveys. It is possible that the high counts obtained during the visual survey may have overwhelmed the observers, but this seems unlikely since there were no differences in the counts of the four observers involved in the survey and similar discrepancies were not seen in surveys of other patches with higher densities of seals or in earlier surveys with the same observers (Stenson *et al.*, 1993). Instead it appears that photographic transects obtained on 14 March overflew areas of high concentrations of animals by chance, thereby resulting in a large estimate with high variance. In contrast, these areas of high seal numbers had less of an influence on the result of the visual survey with its more numerous, closely spaced transects. Thus, there does not appear to be a valid reason to doubt the estimates from either the visual or photographic survey from 14 March and both have been included, along with the subsequent photographic survey, in the final estimate of pup production.

Two estimates were available for N3 and SG1, but in both cases the coverage obtained during the visual survey was incomplete and the photographic surveys were used. A comparison of the N3 survey lines flown on 13 March (visual) and 14 March (photographic) after correction for ice drift, indicated that the photographic transects extended much further west than the visual transects. Since photographs from the non-overlapping area 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 was included in the photographic survey but not in the visual survey. If we assume, however, that pup production in this area was small, there is a good agreement between the visual and photographic surveys of the main concentration.

Female harp seals appeared to be more widely distributed in 1994 than previously reported. This was particularly true of seals off Newfoundland, where whelping has been reported to occur mainly in a few large groups (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, but extensive photographic transects at the Front and in the northern Gulf resulted in good coverage of these areas.

A change in the distribution of whelping harp seals can be illustrated by comparing the results of the 1994 and 1990 surveys. Estimated pup production at the Front was lower (446 700 s.e. = 57 200) than observed during the earlier survey (467 000 s.e. = 31 000; Stenson *et al*., 1993), although the difference was not statistically significant ($p>0.05$). In the northern Gulf, however, pup production rose from less than 1% of the total in 1990 (4400 s.e. = 1300) to 7.5% (57 600 s.e. = 13 700). This may represent a movement of seals from the Front to the northern Gulf. Such movements between areas are likely and Sergeant (1991) reported that whelping concentrations may not form in the northern Gulf ("Mecatina") in some years, but substantial numbers of pups (20 000–35 000) may be born there in others. Pup production in the southern Gulf also changed substantially, increasing from 18% of the total in 1990 (106 000 s.e. = 23 000) to almost 26% in 1994 (200 000 s.e. = 24 200). Winters (1978) estimated that the proportion of the total annual pup production which occurred in the Gulf from 1965–1977 varied between 13% and 51%. We do not know why females appear to move extensively among whelping areas, but changing prey availability or ice conditions may be factors.

The 1994 estimate of total pup production is greater ($p<0.05$) than estimates of pup production for this population in the 1970s and 1980s (Bowen and Sergeant, 1983, 1985; Benjaminsen and Øritsland, 1975; Winters, 1978; Cooke, 1985; Figure 3). However, a direct comparison of these estimates is questionable due to changes in assessment methods since the 1970s and 1980s. The estimates of pup production in both 1990 and 1994 were obtained using similar techniques. A simple test of the hypothesis of no change in pup production (i.e. two-tailed t-test) yields a probability value of 0.06. However, the use of a two-sided alternative fails to take into account other information with respect to the population. As a result of the large reduction in harvesting beginning in 1982, and the general upward trend observed in the historical estimates, an increase in pup production would be expected. The decline in length and mass at age, increase in age at first reproduction and decrease in pregnancy rates that have been reported (Hammill *et al*., 1995; Chabot *et al*., 1996; Sjare *et al*., 1996) are consistent with density dependent changes associated with an increasing population. Accordingly, it would seem more appropriate to test the null hypoth-

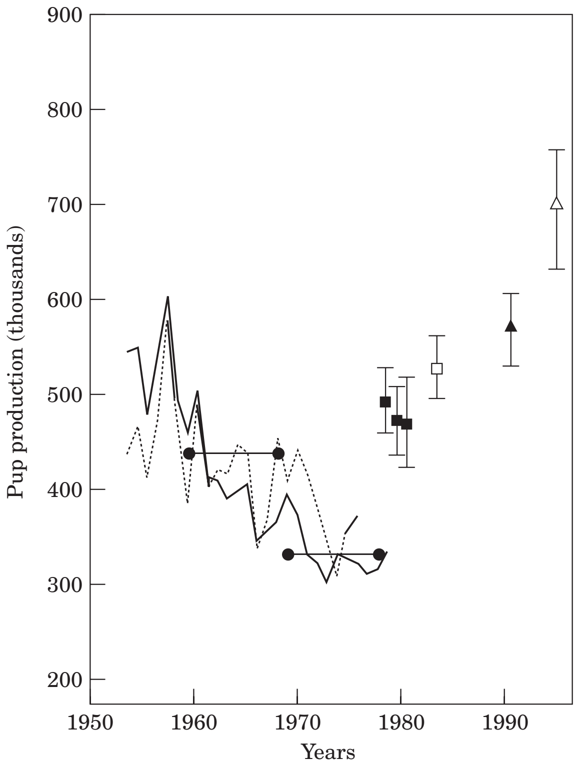

Figure 3. Pup production estimates of harp seals in the northwest Atlantic: cohort analysis by Winters (1978) (——) and Lett and Benjaminsen (1977) (· · ·), average production based on the survival index method by Cooke (1985) assuming moderate ageing errors (●——●), mark recapture estimates by Roff and Bowen (1986) (closed box, ± 1 s.e.) and Bowen and Sergeant (1983) (open box, ± 1 s.e.), and aerial survey estimates by Stenson *et al*. (1993) (closed triangle ± 1 s.e.) and this paper (open triangle ± 1 s.e.).

esis of no increase in pup production against the alternative of an increase (a one-sided alternative, see, e.g. Sokal and Rohlf, 1998). The resulting probability value is 0.03. We conclude that there has been a statistically significant increase in pup production of Northwest Atlantic harp seals since 1990.

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