Abundance of Northwest Atlantic grey seals in Canadian waters

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ABSTRACT

Northwest Atlantic grey seals form a single stock, but for management purposes are often considered as 2 groups. The largest group whelps on Sable Island, 290 km east of Halifax, Nova Scotia. The second group referred to as 'non-Sable Island' or 'Gulf' animals whelps primarily on the pack ice in the southern Gulf of St. Lawrence, with other smaller groups pupping on small islands in the southern Gulf and along the eastern shore of Nova Scotia. Estimates of pup production in this latter group have been determined using mark-recapture and aerial survey techniques. The most recent visual aerial surveys flown during January-February 1996, 1997 and 2000 in the southern Gulf of St Lawrence and along the Eastern Shore resulted in pup production estimates of 11,100 (SE = 1,300), 7,300 (SE = 800) and 6,100 (SE = 900) in 1996, 1997 and 2000 respectively after correcting for births and including counts of pups on small islands. Incorporating information on pup production, reproduction rates and removals into a population model indicates that the Gulf component increased from 15,500 (95% CI = 14,600-16,300) animals in 1970 to 62,700 (95% CI = 49,800-67,800) animals by 1996 and then declined to 22,300 (95% CI = 17,200-28,300) animals in 2000. On Sable Island the population has increased from 4,800 (95% CI = 4,700-4,900) animals in 1970 to 212,500 (95% CI = 159,600-276,200) in 2000. The total Northwest Atlantic grey seal population is estimated to number around 234,800 animals in 2000.

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Fig. 1. *Most grey seals pup on the ice in the Gulf of St Lawrence and in the northern Baltic. This seal is about 2.5 weeks old and beginning to moult. (Photo: Olle Karlsson)*

INTRODUCTION

The Northwest Atlantic grey seal (*Halichoerus grypus*) occurs along the eastern coasts of Canada and United States. In Canada, grey seals form a single population (Boskovic *et al.* 1996), but for management considerations, the population is normally divided into 2 groups; a Sable Island component and a non-Sable Island component. Using pup production as an index of population size and trends, pup production on Sable Island has increased rapidly since the 1970s, from less than 2,000 animals in 1975 to over 25,000 pups in 1997 (Bowen *et al.* 2003) for an annual rate of increase of 12.8%. Less is known about the non-Sable Island component of the Northwest Atlantic grey seal. This component consists of animals that whelp primarily on the drifting pack ice in Northumberland Strait and off the west coast of Cape Breton Island (Figs 1 and 2). Smaller whelping colonies are found on Amet Island, Deadman Island and along the Nova Scotia eastern shore (Mansfield and Beck 1977).

Until 1990, estimates of Northwest Atlantic grey seal abundance were based on the complete tagging and enumeration of pups on Sable Island and on the recapture of non-Sable Island tagged animals (Stobo and Zwanenburg 1990, Hammill *et al.* 1998). However, by 1990, the large numbers of pups born on Sable Island resulted in the complete enumeration technique no longer being feasible. For non-Sable Island animals, low numbers of recoveries reduced the reliability of mark-recapture techniques. As a result, alternative techniques to evaluate abundance were needed.

Aerial surveys have been used successfully to estimate pup production in other pinniped populations (Bowen *et al.* 1987, Hammill *et al.* 1992a. Stenson *et al.* 1993, 2003). These surveys use reconnaissance flights to detect all whelping concentrations in the study area, systematic strip-transect surveys to estimate the number of pups present on the ice and a birth-ogive model to correct aerial survey estimates for the number of pups that are born after the survey has been flown.

Here we apply the aerial survey approach to estimate non-Sable Island grey seal pup production during January-February 1996, 1997 and 2000. These estimates along with earlier mark-recapture estimates of non-Sable Island pup production (Myers *et al.* 1997, Hammill *et al.* 1998), as well as pup production estimates from Sable Island (Stobo and Zwanenburg 1990, Bowen *et al.* 2003), information on reproduction and removals from the population during government-sponsored culling and bounty programs are then incorporated into a population model to determine changes in the Canadian component of the Northwest Atlantic grey seal population over the last 30 years.

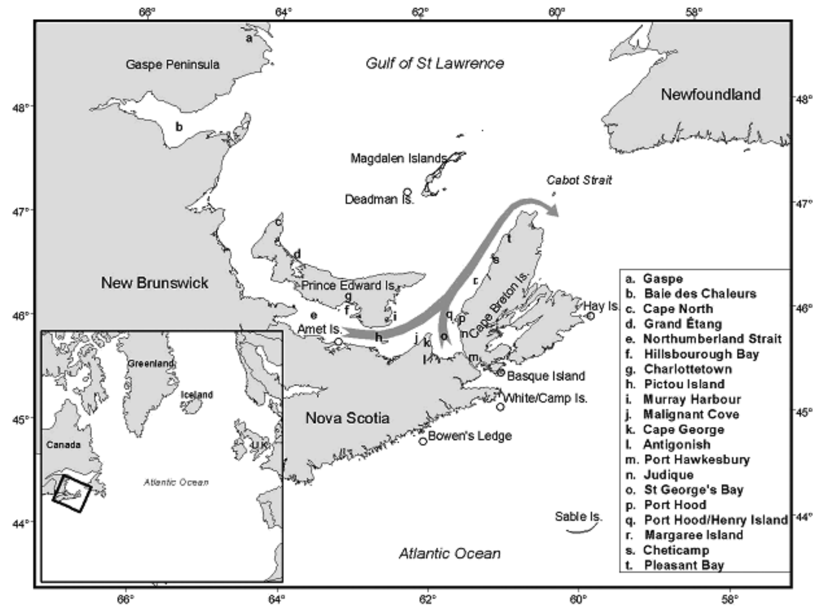

Fig. 2. *Location of whelping grey seal on the ice in the southern Gulf of St Lawrence. The large arrow outlines the main pupping area and direction of ice drift during the survey period.*

MATERIALS AND METHODS

The non-Sable Island component whelps from late December through early February on some small islands in the Gulf of St. Lawrence and along the Nova Scotia Eastern Shore. However, the majority of pups are born on drifting pack ice in the southern Gulf of St. Lawrence (Fig. 2). Ice-breeding grey seals normally prefer medium sized floes (100-500 m across) of white or thin white ice, 15-70 cm thick. Whelping patches are often initially located in the Northumberland Strait between Charlottetown in the west and Cape George in the east. Animals have not been located west of this area. This may be due to colder temperatures along the New Brunswick coast, which may affect pup survival (Hansen and Lavigne 1997) or to the normally much heavier ice conditions in this area. Overall, ice drift occurs from west to east, but short-term changes can occur depending on tidal changes (east to west) and wind action. In some years, strong northerly winds push seals into St. George's Bay, while in others, the ice is pushed rapidly out of the southern Gulf, and exits via Cabot Strait (Fig. 2).

Reconnaissance surveys
Fixed-wing reconnaissance surveys were flown at an altitude of 1,000 feet on 15 January and 1 February 1996 in Northumberland Strait and around Prince Edward Island. These surveys cover coastal areas and ice-covered areas between Prince Edward Island, New Brunswick and Nova Scotia (Fig. 2). In 1997 and 2000 searches for whelping patches were completed by helicopter.

Ice drift was monitored by following the movement of VHF transmitters that were deployed on the ice and by re-sightings of marked groups of tagged seal pups.

Island counts
Counts of pups on the small islands were completed by walking through the colony and tagging all pups, or by slowly flying around the island at an altitude of 30.5 m and at a distance of 71 m from the island and counting all pups on the beach.

Strip-transect surveys
Visual strip-transect surveys were flown at an altitude of 45.7 m by helicopter to estimate the number of pups on the ice. Observers seated in the left and right rear seats counted all seals within a measured strip on each side of the aircraft (50 m in 1996; 75 m in 1997, 2000). The strip was delimited by placing tape marks on the windows while hovering at an altitude of 45.7 m over a measured distance marked out on the ice. Tape marks were also placed on the window to denote the horizon and the outside of the helicopter skid to aid the observer in maintaining a constant position. Following the survey, strip widths were checked again to confirm the areas surveyed.

The data were analysed using the methods outlined in Hammill *et al.* (1992a,b). Survey strata were defined based on groups of transects with homogeneous transect spacing. For each group a weighting factor ki was calculated as:

$$k_i = S_i / W_i \qquad (1)$$

where *Si* is the transect spacing (km) for the ith group and Wi is the transect width (km) for the ith group.

The estimated number of pups for the ith survey is

given by:

$$N_i = k_i \left[\sum_{j=1}^{J_i} x_j \right] \qquad (2)$$

where xj is the number of seals counted on a transect and Ji is the number of transects in the ith survey.

The error variance was calculated based on the serial difference between transects (Cochran 1977, Kingsley *et al.* 1985) using:

$$V_i = \frac{k_i (k_i - 1) J_i}{2(J_i - 1)} \sum_{j=1}^{J_i - 1} (x_j - x_{j+1})^2 \qquad (3)$$

If transect spacing changed the estimate of the number of animals became:

$$N_i = k_i \left[x_{i1}/2 + \sum_{j=2}^{J_i - 1} x_{ij} + x_{iJ_i}/2 \right] \qquad (4)$$

and the variance estimate became:

$$V_i = \frac{k_i(k_i-1)}{2}\sum_{j=1}^{J_i-1}(x_j - x_{j+1})^2 \quad (5)$$

The estimate for the total population and its variance estimate became:

$$N = \sum_{i=1}^{I} N_i \quad (6)$$

$$V = \sum_{i=1}^{I} V_i \quad (7)$$

where I is the number of groups of transects.

Birth ogive

Non-Sable Island Northwest Atlantic grey seals begin pupping on the islands in December and births continue until early February. The majority of births, particularly of ice-breeding animals occur in January. Aerial survey estimates must be corrected to account for births that may occur after the strip-transect surveys are flown. This is done by modelling the distribution of births over the period of the survey. The model assumes that births follow a Normal distribution. It uses the change in the proportion of pups of different ages as the season advances to develop the birthing ogive (details described in Stenson *et al.* 2003). Previous work has indicated that a minimum of 3 stage surveys, and a total of at least 300 pups at each colony or pupping concentration are needed to adequately model the birthing ogive (Stenson *et al.* 2003). Estimates of the number of pups in each concentration can then be corrected for pups born after the survey was flown by:

$$N_i = N_{uncor} / P_i \quad (8)$$

where: N_{uncor} = the uncorrected estimate for survey i; and Pi = the proportion estimated to have been born prior to survey i.

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

$$V_i = N_{uncorr}^2 \times V_p/P_i^4 + V_n/P_i^2 \quad (9)$$

where:
Vp = the variance in the proportion estimated to have been present prior to survey i;
Vn = the variance in the uncorrected estimate for survey I.

Pups were assigned to 1 of 3 distinct age related categories based on a combination of morphometric and pelage features to model the distribution of births. The characteristics and duration of each stage are described by Bowen *et al.* (2003). Stages 1, 2 and 3 had mean durations of 3.4 (SE = 0.91) days, 4.4 (SE = 1.29) and 12.1 (SE = 2.77) days respectively.

The study area was repeatedly surveyed and the change in the proportion of pups in each of the age dependent categories was noted. In all years, stage information was gathered early in the season during tagging operations. Later in the season stage information was gathered by flying random low level transects through the patch. Information on stages was also gathered by a front observer during the strip-transect surveys. In this case only animals passing directly beside the helicopter were assigned to a stage category.

Population model

Estimates of population size and changes in the population over time were determined by constructing a deterministic, age-structured model (Mohn and Bowen 1996). The population numbers N[a;s;y] are described by a 3 dimensional matrix having subscripts a, s, and y for age, sex (m = male, f = female) and year respectively (Mohn and Bowen 1996). The number of pups in any year y is

$$N[0;s;y]=N[0;m;y]=0.5 * \sum N[a;f;y] * (R[a]+\epsilon(a)) \quad (10)$$

Where R is a matrix made up of the age-specific reproductive rates information collected from a sample of shot animals harvested in the early 1990s, and ϵ(a) represents the variability (sampling error) associated with these estimates (Hammill and Gosselin 1995).

Age-specific mortality for animals 1 year of age and older was incorporated into the model using

$$N[a;s;y] = (n_{a-1,s,y-1} - c_{a-1,s,y-1})\ e^{-(\gamma)m} \quad (11)$$

where $-(\gamma)m$ is the mortality rate and c is the age-specific catch during years when culling and bounty hunting occurred (Hammill *et al.* 1998) and including more recent data from animals harvested as part of Department of Fisheries and Oceans diet monitoring studies (Table 1). Mohn and Bowen (1996) assumed that mortality rates were higher for males than for females for animals greater than 5 years of age. However, Mansfield and Beck (1977) reported little difference in mortality rates between sexes up to 20 years of age and more recently (Manske *et al.* 2002, Schwarz and Stobo 2000) reported lower mortality for males than for female in adult breeding grey seals. Therefore we assumed that there was no difference in mortality between males and females <30 years old. An initial population size in 1960, independent estimates of pup production, age-specific reproductive rates and estimates of mortality (Hammill and Gosselin 1995, Hammill *et al.* 1998, Mohn and Bowen 1996, this paper) were used as initial inputs into the model. The 2 management groups were examined separately. For Sable Island, the model was fitted to estimates of pup production from total counts or aerial surveys (Stobo and Zwanenburg 1990, Bowen *et al.* 2003). For the non-Sable Island component, the model was fitted to mark-recapture pup production estimates available from 1984-1990 (Hammill *et al.* 1998) and aerial survey estimates (this study). In 1984, 1985, 1986, 1989 and 1990, several mark-recapture estimates for pup production are available. These estimates were combined to produce a single estimate per year (Mood *et al.* 1974), assuming that samples are independent (Hammill *et al.* 1998).

Table 1. Grey seal removals from the Gulf of St. Lawrence from scientific collections. Juveniles are 1 to 3 years old, and adults are 4 years old and greater.

Year	Pups	Juveniles	Adults
1991	0	0	13
1992	44	119	106
1993	0	1	12
1994	7	11	11
1995	7	2	1
1996	4	10	55
1997	1	2	19
1998	0	0	20
1999	2	11	57
2000	10	14	64

Our data are too limited to consider inter-annual changes in age-specific reproductive rates. We pooled all years and assumed that age-specific reproductive rates followed a normal distribution with mean (standard deviation) of 0.159 (0.19), 0.736 (0.16), 0.834 (0.13), 0.832 (0.15) and 0.907 (0.053) for ages 4, 5, 6, 7, and 8+ years respectively (Hammill and Gosselin 1995). This accounts for some uncertainty in the estimates of the true value (sampling error). For each iteration of the model, a single age-specific value was used over all years, but reproductive rates varied between iterations.

The model was fitted to estimates of pup production weighted by the inverse of the survey variance. Using Risk Optimizer (an Excel spreadsheet add-in from Palisade Corporation 2000), the initial population size and mortality values were adjusted to minimize the mean square differences between estimates of pup production predicted by the model and the observed survey estimates. The model started with an initial population, and mortality rate and sampled from the defined function for reproductive rates 200 times (replicates) and the mean of the sum of squares (MSS) differences was calculated for the 200 replicates. These constituted a simulation. The model stored the MSS value and randomly selected a new initial population size and mortality rate values to carry out a new simulation. After 1,000 simulations, the run with smallest MSS was retained. Once a best fit had been obtained, a new sample of pup production estimates was drawn from the pup mark-recapture and aerial survey data, assuming a Normal distribution with mean and standard error equal to the survey estimates. The model was repeatedly fitted to the drawn pup production estimates to obtain mean and standard error estimates of the initial population and mortality coefficients. Population probability distributions for the population trajectories were then generated by resampling (N

Table 2. Uncorrected pup production estimates, correction factors and corrected pup production estimates for January and February 1996 surveys. Correction factors were not applied to island counts. Standard errors are in parentheses. The final total is rounded to the nearest 100.

Survey Location Date	Counted	Uncorrected estimate	Proportion visible	Corrected estimate
Transect surveys				
Southern Gulf				
24 January	183	2,830 (710)	0.75 (0.07)	3,770 (1,010)
26 January	238	2,790 (380)	0.83 (0.054)	3,360 (510)
27 January	178	860 (170)	0.87 (0.047)	990 (200)
2 February	32	2,100 (580)	0.95 (0.04)	2,210 (620)
St George's Bay				
9 February	41	361 (128)		361 (128)
Sub-total				10,691 (1,306)
Island surveys				
Hay Island				
30 January	395			395
Amet Island				
2 February	26			26
Sub-total				421
Total				**11,100 (1,300)**

= 1,000) from the distributions for reproductive rates, initial population size and mortality rates (@Risk, Palisade Corporation, Newfield, NY).

RESULTS

1996 Surveys

Fixed-wing aircraft reconnaissance surveys were flown only in January 1996 and covered the coastal regions of Prince Edward Island, the west coast of Cape Breton Island, the coasts of New Brunswick and Nova Scotia and the ice areas between Prince Edward Island, New Brunswick and Nova Scotia (Fig. 2). In later years, reconnaissance surveys were limited to traditional whelping areas which include the southeastern portion of the Gulf, and the small islands along the Eastern Shore. Coverage of the west coast of Cape Breton Island and the north coast of Prince Edward Island was limited, due to the absence of suitable ice for whelping, i.e. small to medium-sized pans of white ice.

Visual strip-transect surveys were flown repeatedly during January and February 1996, owing to the discovery of new patches or an inability to cover the whole region in a single day (Fig. 3 a,b,c). The movement of whelping patches was monitored using VHF transmitters deployed on the ice to ensure that successive surveys did not recount the same animals. Transects were oriented north-south or east-west in different regions to be perpendicular to the longest axis of seal patches. Transect spacing also varied within and between surveys ranging from 0.6 km to 5.2 km between transect lines. Transects began about 1 km ahead of seals and ended about 2 km after the last seal was observed or if open water was encountered.

From the movement of the VHF transmitters it was evident that some lines overlapped between subsequent surveys. These lines were removed resulting in an estimated 8,580 animals present in the southern Gulf of St Lawrence in 1996. Another 421 pups were counted on Hay and Amet Islands (Table 2).

Stage surveys were completed between 17 January and 11 February (Table 3). Young animals were detected early in the survey, but as expected this proportion declined as the pupping season advanced. From these surveys, it was estimated

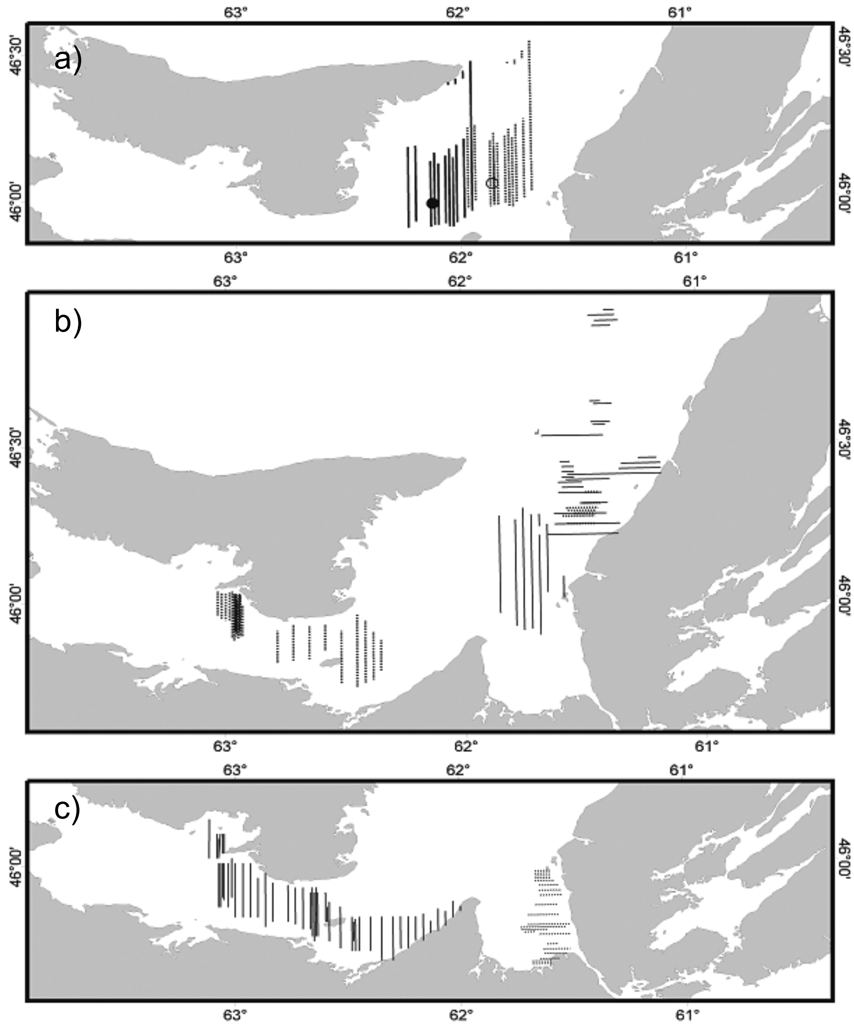

Fig.3.(a) Transects flown and position of VHF transmitter on 24 (solid lines, closed circle) and 26 January 1996 (dotted lines, open circle). (b) Transects flown on 26 and 27 January 1996 (respectively solid and dotted lines). (c) Transects flown on 2 and 9 February 1996 (respectively in solid lines and dotted lines).

that 75% to 95% of pupping had occurred at the time the 24-27 January surveys were flown (Table 2). Correction factors were not applied to the 9 February St. George's Bay and island counts. The low numbers involved and the lateness in the pupping season would suggest that the correction factors for these areas would be small.

Correcting for the distribution of births, adding in the 421 animals counted on Hay and Amet islands increases the estimated pup production to 11,100 (SE = 1,300) (rounded to the nearest 100) in 1996 (Table 2).

1997 Surveys

Ice conditions in January-February 1997 were poorer than those observed in 1996. Much of the southern Gulf and Northumberland Strait area was open-water. Suitable ice did appear in the Strait during the survey period, but open-water conditions were prevalent off Cape Breton Island well into February. Because of this lack of ice, reconnaissance surveys were limited to searching along the coast in Northumberland Strait, along the western Cape Breton coast and along the Eastern Shore by helicopter. Adults and pups were seen along the coast, particularly along the south and west coasts of St. George's Bay, and around the point into Northumberland Strait (Fig. 2). Animals were also seen on the small islands along Cape Breton Island, and on Deadman Island.

Visual transect surveys were flown 22, 26, 28, 29 January and 4 February (Fig. 4 a,b). Counts of pups were also made along the shore of St George's Bay and the west side of Cape Breton Island on 24 January. In 1997, there were an esti-

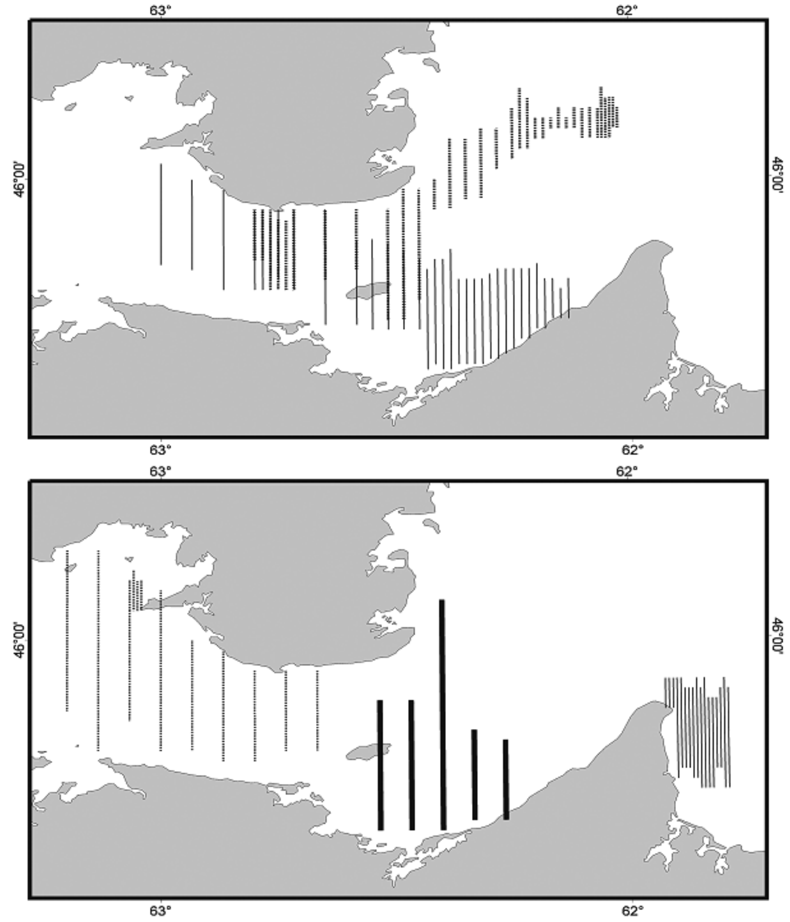

__Fig. 4__. Transects of the 1997 visual survey flown on 22 and 26 January (respectively in bold and thin lines) (top). Transects of the 1997 visual survey flown on 28, 29 January and 4 February (respectively in bold, dotted and thin lines) (bottom).

mated 4,300 pups on the ice from the strip-transect survey (not corrected for births). Another 1,480 pups were recorded on the islands (Table 4).

Stage surveys were conducted between 22 January and 8 February 1997 (Table 5). Animals staged in Group 1, were covered by the strip-transect surveys flown 22, and 26 January. This group also included animals counted along the shoreline in beach surveys flown 24 January. For these surveys it was estimated that pupping was 67-93% complete (Table 4). Animals staged in Group 2, were surveyed 28 and 29 January, pupping was estimated to be 83-88% complete. Animals staged in group 3 were surveyed on 4 February. No corrections were applied to the estimates of group 3 and the number of animals on Hay Island and Deadman Island because of the lack of sufficient staging samples. However, the low numbers involved and the lateness in the pupping season would suggest that the correction factors for these areas would be small.

Correcting the strip-transect surveys for births that occurred after the survey was flown and adding in the number of animals seen on the islands, total non-Sable Island pup production in 1997 is estimated to be 7,300 (SE=800, rounded to the nearest 100) (Table 4).

2000 Surveys

Ice conditions in 2000 were similar to conditions observed in 1997; much of the southern Gulf and Northumberland Strait area were open water. Suitable ice did appear in the Strait during the survey period, but open-water conditions remained off Cape Breton

Table 3. Proportion of pups in various age-dependent developmental stages during the 1996 southern Gulf surveys. Group 1 applies to strip-transect surveys flown 24, 26, and 27 January 1996. Group 2 applies to the strip-transect survey of 2 February 1996.

Group	Date	N	Stage 1 (%)	Stage 2 (%)	Stage 3 (%)
1	17-Jan-96	90	11.1	71.1	17.8
1	18-Jan-96	366	17.8	68.0	14.2
1	21-Jan-96	385	11.9	46.5	41.6
1	22-Jan-96	132	41.7	47.7	10.6
	23-Jan-96	180	49.4	50.0	0.6
1	30-Jan-96	145	0.0	31.7	68.3
1	04-Feb-96	424	0.5	13.9	85.6
1	08-Feb-96	430	0.2	14.9	84.9
2	31-Jan-96	67	44.8	37.3	17.9
2	02-Feb-96	110	5.5	55.5	39.1
2	05-Feb-96	227	0.4	35.2	64.3
2	07-Feb-96	2	0.0	50.0	50.0
2	10-Feb-96	329	0.0	16.1	83.9

Island well into February. Reconnaissance surveys were limited to searching along the coast in Northumberland Strait and along the western Cape Breton coast by helicopter.

Three strip-transect surveys were flown; one in Hillsborough Bay on the south side of Prince Edward Island (23 January), a second in Northumberland Strait (25 - 26 January) and a third along the west coast of Cape Breton Island (28 January). Counts were also made of pups on the small islands in the southern Gulf and along the Eastern Shore (Fig. 5). From the survey with a strip width of 75 m on each side of the aircraft, there were an estimated 4,161 (SE = 728) pups on the ice (not corrected for births). Another 1,209 animals were counted on the island beaches(Table 6).

Stage surveys were flown between 11 January and 11 February 2000 (Table 7, Fig. 5). It was estimated that pupping was 83-99% complete during the surveys (Table 6). Correcting the strip-transect surveys for births that occurred after the survey was flown and adding in the number of animals seen on the islands, total non-Sable Island pup production in 2000 was estimated to be 6,100 (SE=900, rounded to the nearest 100)(Table 6).

Population size

During the survey period between 1984 and 2000 Non-Sable Island pup production increased from around 7,000 animals to a peak of 11,000 animals in 1996 and then has since declined to 6,100 animals(Table 8, Fig. 5) The model was fitted to the pup production survey estimates in 2 steps. The first step fitted to the increasing trend in pup production observed during 1984 to 1996, to obtain estimates of initial

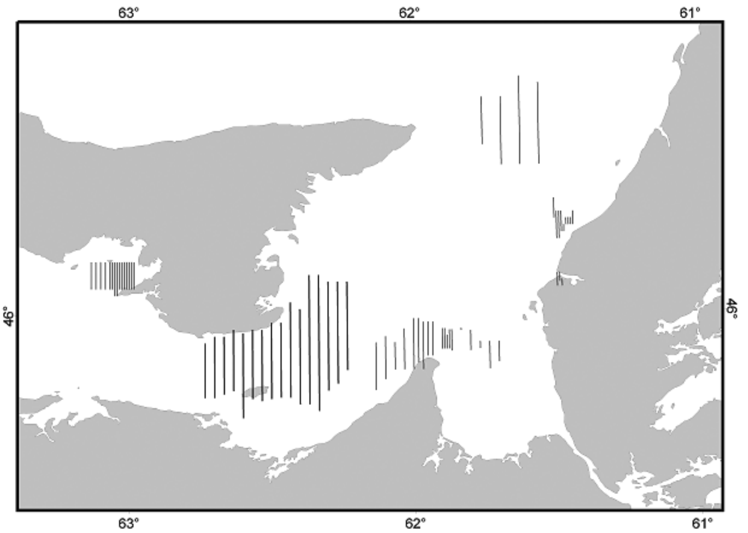

Fig. 5. Aerial survey transects flown in the Gulf of St. Lawrence during January-February 2000.

Table 4. Uncorrected pup production estimates, correction factors and corrected pup production estimates for surveys in January and February 1997. Correction factors were not applied to island counts. Standard errors are in parentheses. Corrected estimates are rounded to the nearest 100.

Survey Location Date	Counted	Uncorrected estimate	Proportion visible	Corrected estimate
Transect surveys				
Northumberland Strait				
22 January	155	1,566 (389.3)	0.67 (0.072)	2,340 (633)
26 January	175	1,721 (372.1)	0.93 (0.045)	1,850 (410)
28 January	4	138 (33.9)	0.83 (0.114)	170 (40)
29 January	62	386 (200.6)	0.88 (0.101)	440 (230)
4 February	94	404 (180.8)	-	400 (180)
Sub-total				5,810 (780)
Island/shore surveys				
Northumberland Strait 24 January[1]	567		0.93 (0.045)	610 (30)
Amet Island 22 January	162			162
White/Camp Island 10 February.	155			155
Deadman Island 31 January	237			237
Hay Island 1 February	906			906
Henry Island 8 February	3			3
Margaree Island 31 January	17			17
Sub-total				1,480
Total				7,300 (800)

[1] Owing to limited ice, some pups were born on the mainland beach. These animals were counted from the air in the same way that aerial island counts were completed.

Table 5. Proportion of pups in various age-dependent developmental stages during the 1997 Southern Gulf surveys. Group 1 applies to surveys flown 22, 26 January. Group 2 applies to surveys flown 28,29 January and 4 February.

Group	Date	N	Stage 1 (%)	Stage 2 (%)	Stage 3 (%)
1	22-Jan-97	404	40.8	58.4	0.7
1	24-Jan-97	886	13.0	71.8	15.2
1	25-Jan-97	3	0.0	0.0	100.0
1	28-Jan-97	293	10.9	44.4	44.7
1	29-Jan-97	458	1.5	30.3	68.1
1	4-Feb-97	20	0.0	15.0	85.0
1	8-Feb-97	611	0.0	4.3	95.7
2	26-Jan-97	36	5.6	86.1	8.3
2	28-Jan-97	60	10.0	81.7	8.3
2	29-Jan-97	201	7.5	74.1	18.4
2	31-Jan-97	63	3.2	38.1	58.7
2	4-Feb-97	67	1.5	35.8	62.7
2	8-Feb-97	175	1.1	25.7	73.1

population size, and mortality rates. This resulted in an initial pup production estimate of 3,000 (95% CI=2,800-3,200) in 1970 increasing to 13,500 (95% CI=10,300-17,300) in 1996. During this period, the total population increased from 15,500 (95% CI=14,600-16,300) in 1970 to 62,700 (95% CI=49,800-67,800) in 1996 for an annual rate of increase of 5.4% per year (Fig. 6). Estimated mortality rates were 0.047 (SE=0.001) for adults and 0.778 (SE=0.004) for pups respectively during the ascending phase. The model was then fitted to the pup production estimates obtained between 1996 and 2000. This resulted in the model estimating a decline in pup production to 4,300 (95% CI=3,200-5,700) in 2000 and a decline in total population to 22,300 (95% CI=17,200-28,300)(Fig 6). In order to achieve this fit, the fitted pup mortality rates increased to 0.802 (SE=0.012), while fitted adult mortality rates increased to 0.408 (SE=0.003).

On Sable Island pup production increased at a rate of 12.8% per year since complete pup counts began in 1977. Fitting the model to the complete count information and 2 aerial survey estimates (Table 9)(Stobo and Zwanenburg 1990; Mohn and Bowen 1996; Bowen *et al.* 2003) resulted in mortality rates for young of the year of m0=0.386 and for animals one year and older m1+=0.035. The model predicts that pup production has increased from about 880 (95% CI=860-900) in 1970 to 40,900 (95% CI=29,300-55,400) in 2000 if no changes in vital rates had occurred (Fig. 7). Total Sable Island population size over that period was estimated to have increased from 4,800 (95% CI=4,700-4,900) to 212,500 (95% CI=159,600-276,200)(Fig. 7).

DISCUSSION

Evaluating abundance of pack ice pinnipeds is challenging because whelping often occurs in remote areas, whelping concentrations are scattered and births are staggered. Aerial surveys have been used successfully to determine pup production in Northwest Atlantic harp and hooded seal populations by using a combination of extensive aerial reconnaissance and correcting for the fraction of pups not on the ice at the time the survey was flown (Bowen *et al.* 1987; Hammill *et al.* 1992 a,b; Stenson *et al.* 1993, 2003). Grey seals differ from harp and hooded seals in that females whelp in small, widely dispersed concentrations during the middle of winter, which makes for short flying days and often poor flying conditions. Furthermore, whelping extends for a longer period of time compared to the other species, beginning in late December and continuing until mid-February. Grey seals, like harp seals, give birth to a white-coated pup that contrasts little with the ice. However, visual surveys have been used successfully to count white pups on the ice provided that attention is paid to the combination of altitude, strip width and flying speed (Stenson *et al.* 1993, 2003). If these conditions are satisfied then survey accuracy depends largely on the detection of all whelping concentrations, monitoring ice drift to ensure that pups are not counted twice and correcting the estimates for the fraction of pups not present on the ice at the time of the survey. We feel that the survey design we used met the requirements for providing accurate estimates of grey seal pup production in the Gulf.

Pup production on the pack ice in the southern Gulf of St Lawrence increased from 6,900 in the mid-1980s to a peak of around 11,100 animals in 1996. Since then, pup production declined to 6,100 animals in 2000. The reasons for this decline are not clear. We do not believe that the surveys are seriously biased for reasons outlined above.

There is no evidence suggesting that animals whelped elsewhere in the southern Gulf. We have not received reports of land-based colonies other than those already known and we have searched in non-traditional areas, such as Baie-de-Chaleur, but no seals have been seen. Information on grey seal movements obtained from satellite tracking over the last decade have not indicated that pupping occurs outside of the regions covered by the reconnaissance flights (Goulet *et al.* 2001).

Overall, there has been a deterioration in ice conditions since 1996, which is expected to have a negative impact on the breeding success of the 3 pagophilic species (harp seals, *Pagophilus groenlandicus*; hooded seals, *Cystophora cristata*, and grey seals) that inhabit this area (Johnston *et al.* 2005). Because of this general deterioration in ice conditions we considered the declines in pup production observed in 1997 and 2000 to reflect a general trend over this period and fitted the population model separately to the 1996-2000 data. In 1997, ice conditions were poor and large numbers of pups were counted along the shoreline in the southern Gulf of St. Lawrence near St. George's Bay. Poor ice conditions were also encountered in 2000. The numbers of animals seen along the Gulf shoreline were greater than in 1996, but not as numerous as observed in 1997. Some animals may have left the Gulf entirely, moving out of the Gulf to pup in other areas along the eastern shore of Cape Breton Island, Nova Scotia or possibly on Sable Island. Movements of animals equipped with satellite transmitters, and tag recoveries indicate that grey seals are very mobile and have little trouble moving in and out of the Gulf in January, and small grey seal pupping colonies are found along the eastern shore of Cape Breton Island and Nova Scotia (Stobo *et al.* 1990, Lavigueur and Hammill 1993, Goulet *et al.* 2001). Visits to these island sites detected some increases, but these visits were limited and animals may have left prior to our arrival, or pupped on the islands after our visit. If we apply the pupping birthogive correction, developed for the ice breeding seals to the island counts, the possible change in island production is not sufficient to account for the observed decline in pup production after 1996. Nonetheless, we likely underestimate total numbers of animals born on the islands, as well as their contribution to the survey variance for these years. One area that we have little information on abundance, but is known as an area where grey seals have pupped in the past are the French Islands of St. Pierre and Miquelon. Some animals may have moved to this area.

In an earlier study, Mohn and Bowen (1996) examined changes in both the Sable Island and Gulf grey seal population between 1967 and 1994. Their study indicated that the Sable Island herd was increasing at an annual rate of 12.8% and numbered 85,300 (95% C.I.

Table 6. Uncorrected pup production estimates, correction factors and corrected (rounded to the nearest 100) pup production estimates for surveys in January 2000. Owing to limited ice, some pups were born on the beach, at Mabou, near Pt. Hood (Fig. 2). These animals were counted from the air in the same way that aerial island counts were completed. Correction factors were not applied to island and shore counts. Standard errors are in parentheses.

Surveys Location Date	Counted	Uncorrected estimate	Proportion visible	Corrected estimate
Transect surveys				
Hillsborough Bay 23 January	143	576 (159)	0.98 (0.008)	590 (160)
Northumberland St 25-26 January	291	3,269 (709)	0.83 (0.059)	3,940 (900)
West Cape Breton Is. 28 January	77	316 (52)	0.99 (0.002)	320 (50)
Sub-total				4,850 (910)
Island/shore counts				
Mabou shore 28 January	167			167
Port Hood Island 28 January	25			25
Henry Island 28 January	65			65
Amet Island 5,8,10 January	153			153
Hay Island 6,10,19 January	711			711
White Island 10 February	88			88
Sub-total	1,209			1,209
Total				6,100 (900)

Table 7. Proportion of pups in various age-dependent developmental stages during 2000 surveys.

Survey	Date	N	Stage 1 (%)	Stage 2 (%)	Stage 3 (%)
Hillsborough Bay	11 Jan	202	48.0	52.0	0.0
	12 Jan	236	60.6	39.4	0.0
	17 Jan	269	20.8	58.0	21.2
	20 Jan	166	6.0	50.6	43.4
	23 Jan	240	0.4	67.5	32.1
	26 Jan	193	0.0	21.2	78.8
	1 Feb	221	0.0	4.1	95.9
	6 Feb	157	0.0	0.0	100.0
Northumberland Strait	20 Jan	216	52.8	46.3	0.9
	23 Jan	312	17.0	81.4	1.6
	28 Jan	300	3.3	72.7	24.0
	31 Jan	694	2.9	33.3	63.8
	6 Feb	192	0.0	12.0	88.0
	11 Feb	45	0.0	0.0	100.0
Cape Breton	28 Jan	142	2.1	49.3	48.6
	6 Feb	498	0.2	0.8	99.0
	10 Feb	80	0.0	0.0	100.0

Table 8. Estimates of Non-Sable or Gulf grey seal pup production, from mark-recapture (M-R) and aerial surveys, rounded to the nearest 100. Standard errors are in brackets.

Year	Anticosti M-R[1]	Sable M-R[1]	Within season M-R study[2]	Aerial survey (this study)
1984	7,000 (1,200)	7,400 (1,400)		
1985	6,400 (900)	7,800 (1,700)		
1986	5,400 (700)	8,600 (2,800)		
1989	10,400 (3,200)	8,900 (2,100)	9,800 (1,000)	
1990	9,200 (2,700)	8,100 (900)	10,500 (1,000)	
1996				11,100 (1,300)
1997				7,300 (800)
2000				6,100 (900)

[1]Hammill *et al.* 1998
[2]Myers *et al.* 1997

78,000-95,000) animals in 1994 (Fig. 8). Our model estimated a 1994 Sable Island population size of 97,100 (95% CI=76,900-120,700), which was slightly higher than suggested by Mohn and Bowen (1996). However, these differences are due in part to the different assumptions incorporated into the 2 models. In the study by Mohn and Bowen (1996), mortality rates for males 6 years of age and older were set almost 3 times higher than that of females. In our study, males and females less than 30 years old were assumed to have the same mortality rates (Mansfield and Beck 1977; Manske *et al.* 2002). When we run the model assuming the differential mortality rate used by Mohn and Bowen (1996), for males 6 years old and older, the estimated population size of 87,800 (95% CI=64,400-111,200) animals is similar to theirs.

For the Gulf component of the population, Mohn and Bowen (1996) estimated a 1994 population size of 68,700 (95% C.I.=42,000-100,000) animals, increasing at a rate of 9% per year. This is higher than our estimate of 53,400 (95% C.I. 43,300-66,000) animals increasing at an annual rate of 5%. The difference results in part

Table 9. Estimates of Sable Island grey seal pup production. Pup production from 1977 – 1990 are total counts (Stobo and Zwanenburg 1990), the 1993 and 1997 are estimates from photographic aerial surveys (Mohn and Bowen 1996[1]; Bowen *et al.* 2003[2]). 95% C.I. are in brackets.

Year	No. of Pups
1977	2,181
1978	2,687
1979	2,933
1980	3,344
1981	3,143
1982	4,489
1983	5,435
1984	5,856
1985	5,606
1986	6,301
1987	7,391
1988	8,593
1989	9,712
1990	11,700
1993	15,000[1]
1997	25,400 (23,500 – 26,900)[2]

from the different estimates of pup production found in Hammill *et al.* (1992b) used by Mohn and Bowen (1996) and the updated estimates of pup production and removals from Hammill *et al.* (1998) for the same period. However, a more important factor is the influence of the 1996 survey estimate on the fitting of the model to the pup production estimates. This estimate lowers both the apparent rate of increase and also the estimated population size in 1994. If we run our model using only the pup production estimates available to Mohn and Bowen (1996), then our model produces an estimated 1994 population of 64,100 (95% CI= 44,300-83,900), which is similar to their estimate.

The Sable Island and Gulf grey seal colonies have had very different population trajectories. These differences likely result from the higher culling and scientific harvests in the Gulf (Stobo and Zwanenburg 1990; Hammill *et al.* 1998), and the higher natural mortality rates experienced by animals in the Gulf of St. Lawrence. In this study, fitted mortality rates for the ascending phase were much higher for pups in the Gulf population, compared to fitted estimates for the Sable Island herd. A higher mortality rate for pups born on the drifting pack ice is consistent with previous studies and reflects the more uncertain conditions experienced by animals using this habitat (Stobo and Zwanenburg 1990; Hammill *et al.* 1998). However, only very slight differences in mortality rates would be expected among adults between the 2 groups. During the declining phase, the much higher adult mortality rates required to fit the model to the observed pup production estimates are an artifact of the fitting procedure. Although some increase in mortality rates might occur, there is also likely some emigration from the Gulf in response to the deterioration in ice conditions.

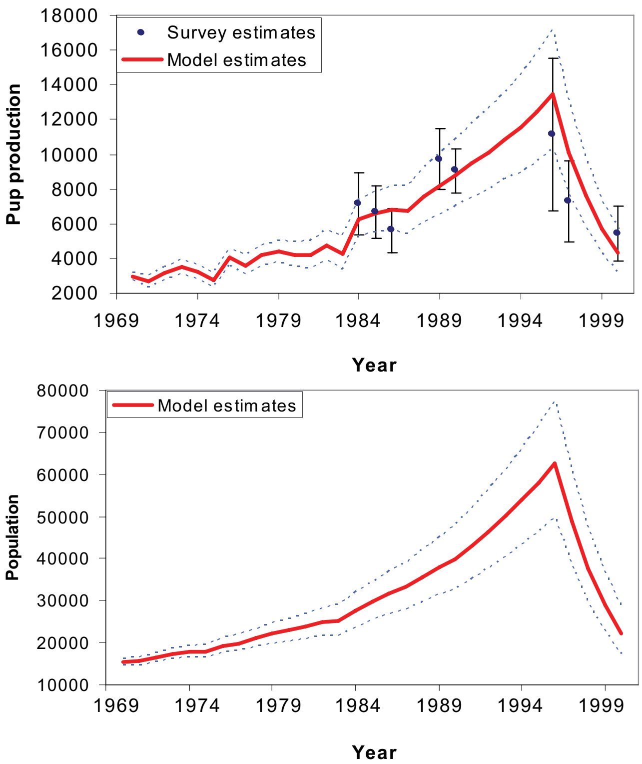

Fig. 6. *Survey (±95% CI) and model estimates of pup production (top) and model estimates of total population size (bottom) for Gulf or non-Sable Island grey seals. Dotted lines represent 95% confidence intervals (CI).*

The higher fitted survival rates for Sable Island in this model are similar to estimates made by Manske *et al.* (2002), for adults

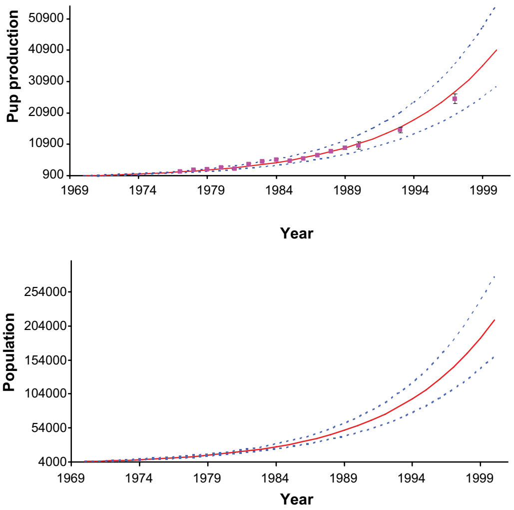

Fig. 7. *Pup counts/survey estimates (±95% CI) and predicted pup production on Sable Island (top) and predicted changes in total population size (bottom) between 1970 and 2000. Dotted lines represent 95% confidence intervals (CI).*

males on Sable Island, but are much higher than rates of 90% estimated by Mansfield and Beck (1977) and rates around 80% in the United Kingdom (Harwood and Prime 1978). Manske *et al.* (2002) suggested that they may have over-estimated survival because their observations focused on animals returning to the breeding colony, and hence may have been influenced by males that were larger, stronger and more aggressive than males not sighted in the breeding colony.

If any net directional movement is occurring with a net loss of animals from the Gulf to Sable Island, then this would contribute to the high rates of increase seen in the latter herd and would also explain some of the differences in fitted adult mortality rate estimates between the 2 groups.

In 1970, the Northwest Atlantic grey seal population numbered around 30,300 (SE=200) animals of which approximately 80% were of Gulf origin. Since that time, the Northwest Atlantic grey seal population has increased, particularly on Sable Island. Total population in 2000, probably numbers around 246,500 (SE=31,500) animals, with the Sable Island component making up about 77% of that total.

Fig. 8. A crowded beach on Sable Island. (Photo: Yves Morin)

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