

REDUCED POPULATION GROWTH OF GRAY SEALS AT SABLE ISLAND: EVIDENCE FROM PUP PRODUCTION AND AGE OF PRIMIPARITY

W. D. BOWEN

J. I. McMILLAN

Population Ecology Division,
Bedford Institute of Oceanography,
Department of Fisheries and Oceans,
Dartmouth, Nova Scotia B2Y 4A2, Canada
E-mail: bowend@mar.dfo-mpo.gc.ca

WADE BLANCHARD

Mathematics and Statistics Department,
Dalhousie University,
Halifax, Nova Scotia B3H 3J5, Canada

ABSTRACT

Pup production on Sable Island, Nova Scotia, has been increasing exponentially since the early 1960s and by 1997 Sable Island was the largest gray seal colony worldwide. Using an aerial photographic survey, as in previous years, we estimated pup production in January 2004 to determine if this exponential rate of increase had continued. A total of 33,268 pups was counted on the color positives. When corrected for the proportion pups missed on the imagery (1.106 for the 12th; 1.527 on the 13th), the proportion of pups that died prior to the survey (0.031), and the proportion of pups born before the survey (east colony 0.966, west colony 0.962), estimated total pup production was 41,500 with $SE = 4,381$. The 2004 estimate indicates that pup production on Sable Island has continued to increase, but suggests that the rate of increase (r) may have declined (0.070 compared to previous 0.128). Females from the 1998–2000 cohorts were about 16 times less likely to give birth for the first time at age 4 yr and more than twice as likely at age 6 yr compared to those in the mid-late 1980s. The new estimate of pup production and observed changes in age of primiparity provide the first indication of changes in vital rates of this population. However, additional estimates of pup production and vital rates are needed to confirm this conclusion and to investigate the underlying mechanisms.

Key words: population dynamics, pinniped, reproduction, gray seal, *Halichoerus grypus*.

Large mammals have several life history traits that generally result in low intrinsic rates of population increase. They are long-lived, females take many years to mature,

and litter size is low (Fowler 1981). In the case of pinnipeds, rates of increase have been estimated in relatively few species from long-term measurements of population size, or more usually from surveys of pup production. One of the longest series of estimates of pup production comes from a study which began in 1962 at Sable Island, Nova Scotia. The number of gray seal (*Halichoerus grypus*) pups born at Sable Island has increased exponentially for the past four decades (Bowen *et al.* 2003). This sustained increase in pup production, and by inference population size, has resulted in increased prey consumption, which, among other ecosystem effects, may negatively impact marine fish populations of commercial importance (Mohn and Bowen 1996, Fu *et al.* 2001). In particular, the continued decline in the eastern Scotian Shelf stock of Atlantic cod (*Gadus morhua*), despite a moratorium on fishing over the past 12 yr, has raised concern about the sources of mortality, including seal predation, which may be preventing recovery of this stock (Trzcinski *et al.* in press). The sustained population growth of gray seals over many decades also provides an opportunity to examine the extent to which the dynamics of a large marine carnivore are linked to long-term changes in marine continental shelf ecosystems (*e.g.*, Bowen *et al.* 2006).

The gray seal is a generalist predator feeding on a wide range of demersal and small pelagic fishes (Bowen and Harrison 1994) in continental shelf ecosystems and inland seas on both sides of the North Atlantic Ocean. Within its Canadian range, the gray seal forages widely throughout the Scotian Shelf and the Gulf of St. Lawrence during the non-breeding season (Stobo *et al.* 1990, Bowen *et al.* 2006). Major gray seal breeding colonies are located on the sea ice in the southern Gulf of St. Lawrence and on Sable Island, Nova Scotia. Smaller colonies are found on near-shore islands off Cape Breton and along the eastern shore of Nova Scotia (Mansfield and Beck 1977, Hammill *et al.* 1998).

Here we report on the 2004 aerial photographic survey of gray seal pup production at Sable Island. Our objective was to test the hypothesis that gray seal production has continued to increase at a rate near the estimated maximum intrinsic rate of increase (r_m) for this species. Using long-term life history data from individually marked females, we also examined trends in age of primiparity, a trait which is thought to be a relatively sensitive indicator of density-dependent changes in vital rates (Eberhardt 1977).

METHODS

The estimation of pup production follows the approach given in Bowen *et al.* (1987), Myers and Bowen (1989), and Bowen *et al.* (2003). The number of pups born prior to the aerial survey is based on counts of live pups photographed. This number is then corrected for the fractions of live pups not detected on the imagery, pups that had died prior to the survey and hence were not visible on the imagery, and pups that were born after the survey was conducted.

More of the island has been used by lactating females as pup production has increased over time, such that by 2004 pups were born along the entire length of the island. Thus, for the first time in our survey series, the entire island was photographed in 2004. The photographic survey was conducted using an A-star helicopter over 2 d with most of the island photographed on 12 January between 1009 and 1409 (Atlantic standard time), and the balance photographed on 13 January between 13:43 and 14:21. The helicopter was equipped with a radar altimeter and motion compensation camera housing. Photographs were taken with a Jena LMK 15

camera equipped with a 152.160-mm lens, clear filter, and Aviphot Chrome 200 PE1 color-positive film, as in Bowen *et al.* (2003). Twenty-eight transects were flown at an altitude of 800 ft (246 m) to provide complete photographic coverage of the island. Individual photographs had about 30% forward overlap and adjacent transects had 20% lateral overlap and a resolution of 0.25 m.

Prior to reading the photographs, mosaics of adjacent photographs were constructed and areas of overlap were identified and marked on clear acetate sheets to avoid double counting. Each photographic positive was examined over a light table using an illuminated hand lens (7 X magnification). The number and position of pups were recorded on a clear acetate overlay by circling images on the positives. A single experienced reader examined color positives twice after a period of training on selected photographs and training was continued until consistent counts were achieved.

Pup Production Estimates

Total pup production was estimated as follows:

$$N_{total} = \sum_{i=1}^2 \sum_{j=1}^2 \left(\frac{count_{ij} \bullet g_j}{(1-d) \bullet p_i} \right), \quad (1)$$

where $i = 1$ and 2 for the east and west colonies, respectively, $j = 1$ and 2 for photographs taken on the 12th and 13th, respectively, and *count* is the count of live pups on the positives, p is the estimated proportion born prior to the time of the survey in each stratum, g is the estimated ground-count correction, and d is the estimated proportion of pups that had died up to the day of the photographic survey. Standard error (SE) of total pup production was calculated from the estimated variances of correction factors using the delta method for independent random variables (Appendix). Although pups were born over the entire island in 2004, we retained the separate estimation for the west colony and the east colony because there was clear break in the spatial distribution of pups near the Weather Station at the western end of the Island.

The proportion of live pups that were photographed but not detected on the positives (g) in Equation (1) was determined by comparing pups counted in the photographed ground plots to the number of pups counted by observers on the ground. The nine rectangular ground plots were located throughout the east colony in all three major habitats: beach, vegetated dunes, and dune edges. Classification of these habitat types was rather subjective and they were selected to capture what was thought to be an important source of variability in the ability to detect pups on the imagery. However, the intention was not to stratify the estimate on the basis of habitat type. The corners of each plot were demarcated with red vinyl fabric enabling us to locate the plots on the color positives. The size of the plots varied so that each plot contained >25 pups. Two researchers on the ground counted pups independently as close as possible to the time the survey aircraft was overhead. Differences between observers were resolved before going to the next plot.

Temporal Distribution of Births

Two kinds of information were used to model the temporal distribution of births

over the course of the season: the duration of developmental stages of pups and temporal changes in the proportions of each developmental stage. Pups were classified into five developmental stages based on a combination of pelage coloration and body shape (Bowen *et al.* 2003). These stages were similar to those defined by Radford *et al.* (1978) and Kovacs and Lavigne (1986). We assumed stage durations were the same in 2004 as those measured in 1997 on Sable Island (Bowen *et al.* 2003). To estimate how the proportion in each developmental stage changed over time, we recorded pup stages at weekly intervals over the course of the breeding season at nine sites (different than the ground plots referred to above) on the island using the same method as in Bowen *et al.* (2003).

We estimated the temporal distribution of births using the method described in Bowen *et al.* (2003), based on the approach developed by Myers and Bowen (1989). We assumed a population in which the birth rate in a year can be adequately described by a continuous function of time, $m_1(t)$, which we call the temporal distribution of births. The function $m_1(t)$ was discretized because pups were counted periodically, not continuously. Pups pass through a series of identifiable age-dependant stages. Stages are denoted by the subscript j , and if an animal survives it passes from stage j to $j + 1$. Stage duration is specified in terms of transition intensity functions, $\phi_j(\tau)$, the probability that an animal passes from stage j to $j + 1$ in the interval $[\tau, \tau + 1]$ and has survived, where τ is the time spent in stage j . We assumed that stage duration is a semi-Markov process, *i.e.*, the transition intensities depend only on the current stage and the time so far spent in that stage. The rate at which pups enter stage j at time t is denoted by $m_j(t)$.

We assumed that mortality rate between stages was small enough that it could effectively be ignored, such that the rate at which a pup enters successive stages is given by the recurrence relationship:

$$m_j(t) = \sum_{\tau=0}^{\infty} m_{j-1}(t - \tau) \phi_{j-1}(\tau). \quad (2)$$

The total number of pups in stage j at time t , $n_j(t)$, is the sum of the product of the rate pups entered stage j time τ ago times the probability that those pups have not entered the next stage $j + 1$:

$$n_j(t) = \sum_{\tau=0}^{\infty} m_j(t - \tau) \left[1 - \sum_{s=0}^{\tau} \phi_j(s) \right], \quad (3)$$

where s is the time interval of summation.

Equations (2) and (3) adequately describe stages 1–4 because pups are always visible during these stages. By stage 5 however, pups begin to enter the water temporarily. Let $\mu(t)$ be the proportion of stage 5 pups that are in the water time t after the transition from stage 4. Equation (3) can be modified to describe the number of stage 5 pups visible at time t .

$$n_5(t) = \sum_{\tau=0}^{\infty} \mu(t - \tau) m_5(t - \tau). \quad (4)$$

Because stage 5 is the final stage during our study, the $(1 - \sum_{s=0}^{\tau} \phi_j(s))$ term is not required.

The proportion of pups in each stage is estimated according to Myers and Bowen (1989). In discrete form, the proportion of pups available to be photographed (p_a) at time t_i becomes

$$p_a = \frac{\sum_{j=1}^5 n_j(t_i)}{\sum_t m_1(t)}, \quad (5)$$

where the summation indicated by t is over the entire season of births.

We considered three distributions for the number of pups born over time (Table 1) and in all parameterizations, ρ is the scale parameter and κ is the shape parameter. We selected the model with the lowest Akaike's Information Criterion (AIC) and highest Akaike weight (Burnham and Anderson 2001).

Pup Mortality Rate

To estimate the fraction of pups that may have died prior to the photographic survey, we regularly (\sim every 3 d) counted and marked the number of dead pups in another nine sites. These were well-defined areas of the colony selected because they were clearly demarcated such that the number of live pups photographed on the day of the survey could be determined.

Age of Primiparity

Recently weaned (*i.e.*, within \sim 2 wk) gray seal pups were hot-iron branded with individual marks in 1985, 1986, 1987, and 1989 and again from 1998 through 2002. These branded females provided an opportunity to determine the age at first birth for individuals recruiting to the breeding population on the island. Females were judged to be primiparous if they had not previously been seen during a breeding season and were either observed pregnant or nursing the first breeding season they were sighted. Non-pregnant females are rarely seen among lactating females and fostering is also rare on Sable Island (Perry *et al.* 1998), so we can be reasonably confident that the first year a female was observed, she was primiparous.

To determine if a branded female had returned to Sable Island during the breeding season, we conducted weekly censuses of the entire colony. Censuses were conducted by 4–8 researchers and the use of all terrain vehicles ensured that the colony was thoroughly searched. Typically, five or six censuses were conducted each year covering the entire season of births. Although some of the females branded on Sable Island as pups may give birth at other colonies, gray seals exhibit strong philopatry at other

Table 1. Models used to fit the distribution of births over time.

Distribution	Density function	Number of parameters
Gamma	$\rho (\rho t)^{\kappa-1} \exp(-\rho t)$	2
Weibull	$\kappa \rho (\rho t)^{\kappa-1} \exp[-(\rho t)^\kappa]$	2
Log-Logistic	$\kappa \rho^\kappa t^{\kappa-1} [1 + (\rho t)^\kappa]^{-2}$	2

ρ = scale; κ = shape parameter.

colonies (Pomeroy *et al.* 1994), including Sable Island (W. Stobo, unpublished data). Furthermore, Sable Island is by far the largest colony in the Northwest Atlantic and therefore we expected that most females would return to Sable Island to give birth for the first time. Although the number of females giving birth in Sable Island has increased dramatically, in 2004 there was still unoccupied habitat and other areas where the density of females was low such that there is no reason to expect that young females from the 1998 to 2002 cohorts would be excluded from the breeding colony.

Statistical analyses were preformed using S-plus version 6.2 and SPSS version 11.5. The SE is given as a measure of variability about means.

RESULTS

The aerial survey was conducted over 2 d and yielded a count of 33,268 pups, 6,368 pups (19.1%) on 196 positive images (photographic lines 1–7) of the west colony and 26,900 pups on 719 positives (lines 8–28) of the east colony. Most photographs (704 of 915 or 76.9%) were taken on 12 January, accounting for the majority of the pups counted (85.6%). The remainder of the pups (*i.e.*, 4,802) was photographed on 13 January. Weather on both days was not optimal for the survey. January 12th, the better of the two days, was bright overcast with light winds, but a light covering of recent snow made the identification of pups more difficult. Additional light snow fell overnight and 13 January was darker overcast resulting in poorer quality photographs.

Correction for Non-Detection of Live Pups

The nine ground-control plots contained from 29 to 74 pups (Table 2). Correction factors (ground count/counts from positives) varied from 1.03 to 2.21 and were greater for the vegetated plots than for the other two habitats. However, two of the three vegetated plots were photographed on the 13th, but the ground counts were conducted the day before. Further, as noted above, the quality of the photographs was poorer on the 13th than on the 12th. The photograph-quality effect was also evident

Table 2. Number of gray seal pups counted on 9 ground plots (G) and from color positives (P) of those plots (Δt : time difference between G and P). Standard error given in parentheses.

Habitat	Location	Date	Δt (min)	Number of pups counted		G/P
				(G)	(P)	
Sand beach	East light dune	12/01	42	74	67	1.10
	CWS	12/01	30	68	60	1.13
	West washover	12/01	30	44	39	1.13
Vegetated	Stepple flat	13/01	~1 d	34	16	2.12
	Long dune	13/01	~1 d	49	28	1.75
	Tern colony	12/01	65	41	36	1.14
Dune edge	Lakeshore	13/01	~1 d	29	24	1.21
	High ground	13/01	~1 d	34	33	1.03
	East light cut	12/01	49	36	35	1.03
12th						1.106 (0.020)
13th						1.527 (0.250)

in the higher correction factor for the dune-edge habitat plot at the Lakeshore site than for the other two plots in this habitat that were photographed the day before (Table 2). Although, our interpretation of habitat differences is confounded both by imagery quality and timing of ground counts, there was clear evidence of a date effect and thus we used a different correction factor for photographs taken on the 12th and the 13th (Table 2).

Distribution of Births

The developmental stage of 9,615 pups was recorded along ground transects at the nine sites over a 30-d period (Fig. 1, Table 3). Two of these sites were located in the west colony and seven were located in the east colony. Three models were fitted to estimate the distribution of births over time and from that the proportion of pups

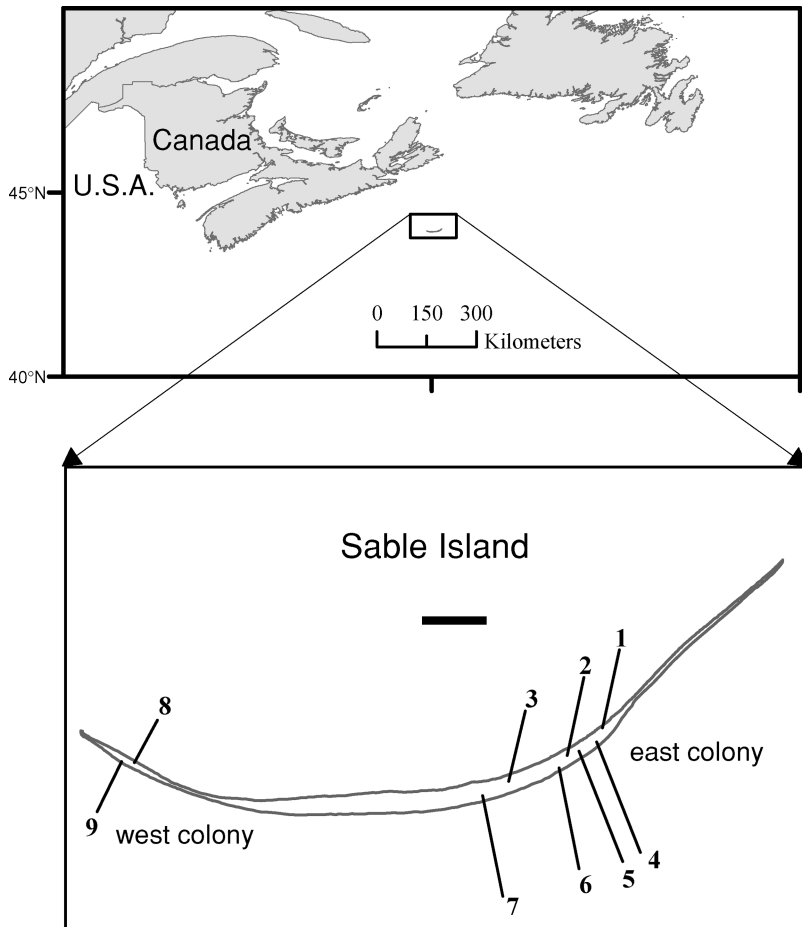


Figure 1. Map showing Sable Island and the location of ground plots used to correct the total count for pups not seen in the imagery. Site names and data given in Table 2.

born by 12 January (Table 4). We estimated the date of the first birth as 5 December and 10 December for the east and west colonies, respectively, based on the oldest stage pups observed on our arrival on 22 December, to define the limit of the left tail of the modeled distributions. All models did not fit the early season proportions of stages 1 and 2 or the later season proportions of stage 3 particularly well (Fig. 2). Based on the AIC criteria, we used the results from the Weibull model to estimate the proportion born in both west and the east colonies (Table 4).

There might be several reasons why the models did not fit the data well in 2004 including a change in the duration of stages since that last estimates were made (*i.e.*, 1997, Bowen *et al.* 2003). We explored this possibility by reducing the duration of stage 1 and increasing the duration of stage 2. Parameters in the known-age, pup stage duration model were fit with a gamma model that had a common shape parameter (21.218) and separate rate parameters for each stage (5.46, 5.25, 2.02, 3.01) for stages 1–4, respectively. Thus, the average time spent in stage 1 is $21.218/5.56 = 3.8$ d, and the average time spent in stage 2 is $21.218/5.25 = 4.0$ d. We increased the rate parameter for stage 1, such that the average duration spent in stage 1 was reduced to $21.218/7 = 3.0$ d and decreased the rate for stage 2, such that the average duration spent in stage 2 was increased to $21.218/2.5 = 8.5$ d. Although these new values give a qualitatively better fit to the actual birthing distribution observed in the present study, they are illustrative only as we do not know that such changes occurred. Nevertheless, changes in stage duration of this magnitude had a small effect (<4%) on the estimate of the proportion born prior to the survey. Thus, the poor fit to several of the pup stage proportions had little effect on the overall estimate of pup production.

Pup Mortality Rate

The nine sites selected to estimate the proportion of pups that had died before the photographs were taken accounted for about 20% of the live pups photographed. The proportion that had died varied from 0.017 to 0.054 (Table 5) with a mean of 0.031 ± 0.004 ($n = 9$).

Total Pup Production

Estimated N_{total} was 41,500 (SE = 4,381) with approximate 95% confidence limits of 33,800 and 51,000 (based on log-normal distribution) (Table 6).

Changes in Age of Primiparity

The number of females giving birth for the first time at age 4, 5, and 6 differed significantly among cohorts ($\chi^2 = 79.7$, $df = 12$, $P < 0.001$). Examination of adjusted residuals from this analysis revealed that significantly fewer 4-yr-olds gave birth in recent (1998–2000) compared to the 1980 cohorts and significantly more 6-yr-olds than expected (Table 7). Expressed as odds ratio, females were about 16 times more likely to give birth for the first time at age 4 during the mid to late 1980s than they were from 1998 to 2000. By contrast, females were more than twice as likely to give birth for the first time at age 6 yr compared to the mid to late 1980s cohorts.

Table 4. Estimates of the proportion of pups born by 12 January 2004 based on three model fits for east colony (sites 1–7) and the west colony (sites 8–9). Standard error given in parentheses. All models had 2 parameters.

Date of first birth	Colony	Model	Shape	Rate	Proportion born	AIC	Akaike w
5 Dec	East	Log-Logistic	3.19 (0.150)	0.045 (0.002)	0.854 (0.020)	17,798.98	0.0
		Gamma	4.72 (0.392)	0.210 (0.020)	0.919 (0.014)	17,766.48	0.0
		Weibull	2.64 (0.099)	23.97 (0.619)	0.966 (0.008)	17,706.36	1.0
10 Dec	West	Log-Logistic	4.10 (0.745)	0.046 (0.002)	0.849 (0.055)	5,303.24	0.0
		Gamma	6.81 (2.079)	0.308 (0.103)	0.894 (0.042)	5,325.26	0.0
		Weibull	3.45 (0.343)	23.42 (0.778)	0.962 (0.021)	5,237.54	1.0

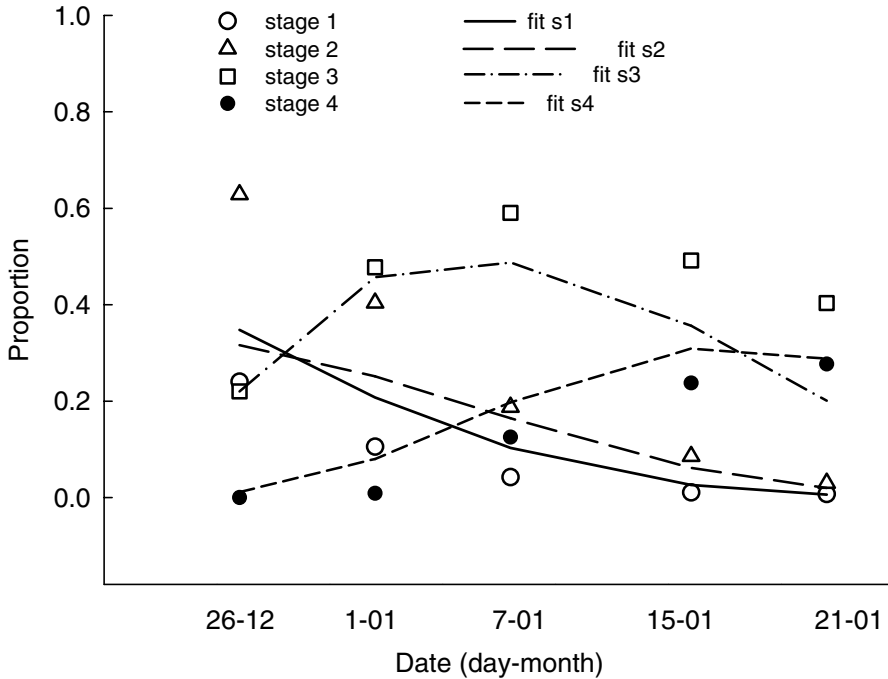


Figure 2. Observed and model estimates for stages 1–4 in the east colony (Weibull distribution, see Table 3) of the proportion of each pup stage throughout the breeding season in 2004 in the east colony and the west colony.

DISCUSSION

Pup production of gray seals at Sable Island has increased exponentially at a rate near r_m for four decades (1962–1997; Bowen *et al.* 2003). Extrapolating the exponential model (Bowen *et al.* 2003) using the most accurate series of pup cohorts (*i.e.*, 1976–1997) gave a predicted 2004 pup production of 60,900 with 95% confidence limits of 48,200–76,900 (Fig. 3). Although the 2004 estimate is well below that predicted

Table 5. Estimates of the fraction of pups that died up to 7 January at nine sites on Sable Island.

Location	Number dead	Live pups	Proportion dead
Beck's Cove	5	167	0.030
Blowout	33	1,268	0.026
CWS	16	549	0.029
East Light, north beach	49	1,082	0.045
East Light cut, N	4	238	0.017
Lakeshore	44	1,395	0.032
Legal Crossing, E	21	1,392	0.015
No. 4 West	13	239	0.054
No. 4	11	311	0.035

Table 6. Estimate of gray seal pup production on Sable Island in 2004 with SE in parentheses.

	West colony	East colony	Sable total
Pup counts from positives	6,368	26,900	33,268
Number photographed 12th/13th	6,368/0	22,098/4,802	
Ground-count correction 12th/13th	1.106/-	1.106/1.527	
Proportion born 12th	0.962	0.966	
Dead pup correction	0.969	0.969	
N_{total}	7,555 (362)	33,959 (4,366)	41,500 ^a (4,381)

^a Rounded to the nearest hundred.

based on rate of increase in pup production through 1997, the confidence limits (33,800–51,000) of the 2004 estimate do slightly overlap those of the prediction. Nevertheless, a two-sample z -test indicated that the two estimates were significantly different (both estimates \ln -transformed, $z = 2.44$, $P = 0.007$.) The rate of increase between 1997 and 2004, calculated as $\{\ln(N_{2004}/N_{1997})\}/7$, was estimated at $r = 0.070$ compared to the previous rate of $r = 0.128$.

Sources of Error in Estimated Pup Production

Pup counts from the imagery must be corrected for several factors to estimate total pup production. First, some live pups may be missed on the positives. Light snow cover and overcast conditions during the survey resulted in generally lower-quality imagery than that in 1997. Our counts of pups in ground plots indicated that the reader missed about 11% of the pups present on the 12th but 53% on the 13th. Ground counts were conducted on the 12th in anticipation that all plots would be photographed on the day. However, we were unaware that several plots were not photographed until the 13th. Therefore, we have less confidence in the estimates for the 13th as there may have been some movement of females and their pups with respect to the plot boundaries during the intervening 24 h and image quality was poorer in the 13th. As estimates of the fraction missed from the 12th were comparable to our 1997 data, this suggests that the poorer image quality on the 13th accounted for the higher fraction of pups missed on that day. Thus, our decision to use different correction factors for each day of the 2004 survey seems justified. Second, pups that died before the aerial survey was conducted will not have been counted. On Sable Island, drifting sand and snow soon cover dead pups making them invisible on the positives. We corrected for pup mortality, however, our correction again may have underestimated the true mortality rate, and thus total pup production, because the last count of dead pups was 5 d before the survey was conducted due to poor weather. However, given that the correction of dead pups was $\sim 2\%$ in 1997 (Bowen *et al.* 2003) and our estimate in 2004 was 2.9%, it seems unlikely that this source of error would significantly affect our estimate of total production. Finally, lack of fit of the birth distribution model, perhaps due to changes in stage duration, suggests that we might have underestimated production. It is difficult to estimate the extent of such a bias, but as indicated in the Results, the bias is likely $< 4\%$.

Table 7. Number (*n*) and percentage (of total) of primiparous gray seal females observed at ages 4, 5, and 6 yr from cohorts branded in 1985 through 2000.

Cohort		Age (yr)			Total observed
		4	5	6	
1985	<i>n</i>	25	98	48	171
	Expected	34.4	87.1	49.4	
	%	14.6	57.3	28.1	
	Adjusted residual ^a	-2.0	1.9	-0.3	
1986	<i>n</i>	63	80	44	187
	Expected	37.6	95.3	54.1	
	%	33.7	42.8	23.5	
	Adjusted residual	5.3	-2.5	-1.8	
1987	<i>n</i>	42	70	53	165
	Expected	33.2	84.1	47.7	
	%	25.5	42.4	32.1	
	Adjusted residual	1.9	-2.5	1.0	
1989	<i>n</i>	34	93	27	154
	Expected	31.0	78.5	44.5	
	%	22.1	60.4	17.5	
	Adjusted residual	0.7	2.6	-3.5	
1998	<i>n</i>	0	17	14	31
	Expected	6.2	15.8	9.0	
	%	0.0	54.8	45.2	
	Adjusted residual	-2.8	0.4	2.0	
1999	<i>n</i>	0	40	35	75
	Expected	15.1	38.2	21.7	
	%	0.0	53.3	46.7	
	Adjusted residual	-4.6	0.4	3.6	
2000	<i>n</i>	3	25	19	47
	Expected	9.5	24.0	13.6	
	%	6.4	53.2	40.4	
	Adjusted residual	-2.4	0.3	1.8	
Total		167	423	240	830

^a Difference between the observed count and the expected count/residual's standard error normalized to a variance = 1. Values below -2 and above 2 indicating departure from independence are given in bold font.

Trend in Pup Production

A decrease in the rate of increase of pup production on Sable Island could have been caused by density-dependent changes in vital rates. Another possibility is that 2003 was simply a bad year (perhaps low food abundance) such that fewer females gave birth in 2004. However, estimated groundfish and pelagic fish biomass in 2003 on the Scotian Shelf (Frank *et al.* 2005), a primary foraging habitat for this gray seal population, was similar to previous years thus arguing against this hypothesis. Nevertheless, one must be cautious in drawing conclusions on the basis of a single estimate. Additional estimates of pup production will be required to determine if the 2004 estimates truly marks a change in the rate of increase.

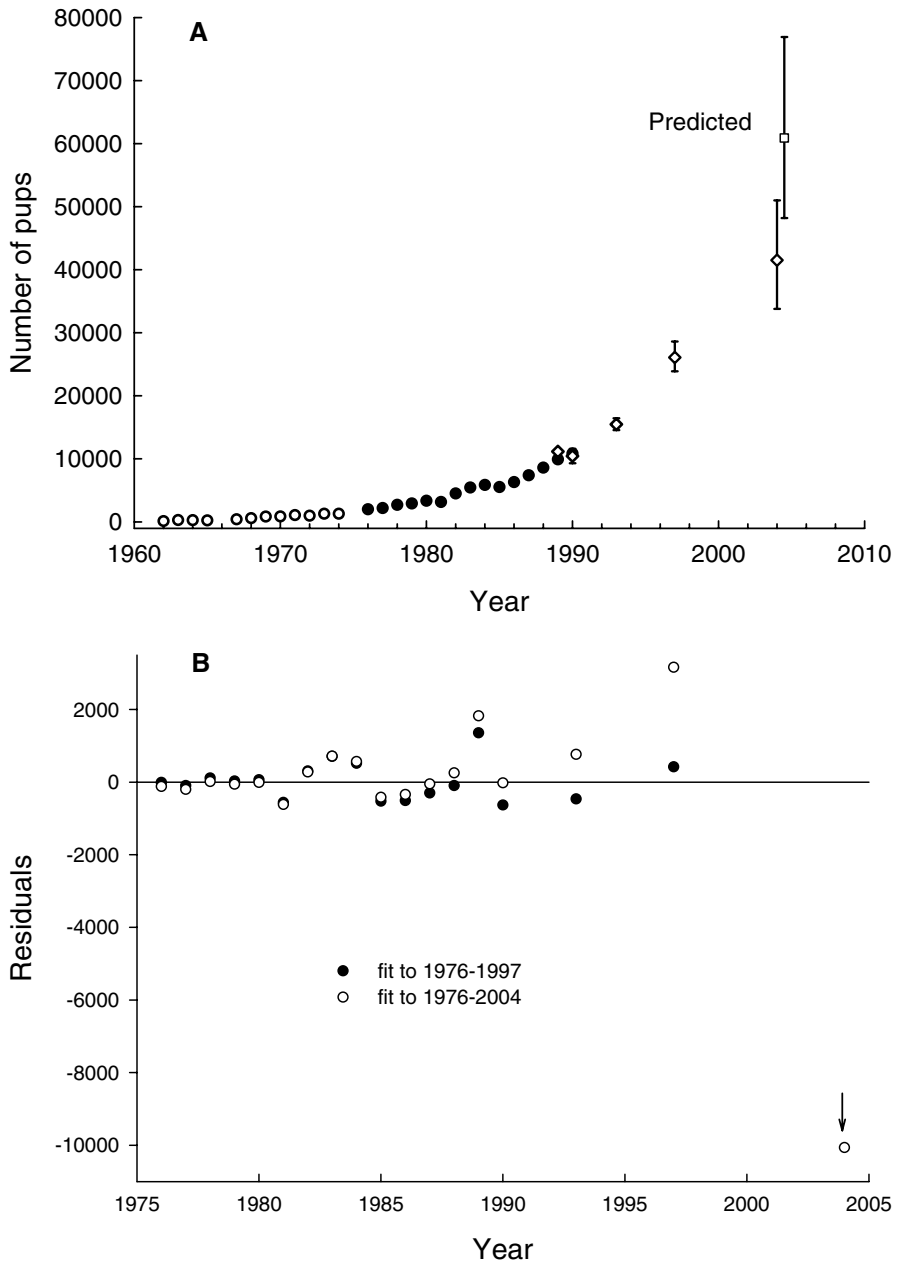


Figure 3. (a) Trend in gray seal pup production on Sable Island, 1962–2004, based on incomplete tagging (1962–1974), complete cohort tagging (1976–1990), and aerial photographic surveys (1989–2004). Error bars are approximate 95% confidence limits. Open square is predicted pup production in 2004 (staggered by 0.5 yr) from an exponential model in Bowen *et al.* (2003), (b) Residuals from exponential fits to the 1976–1997 and to the 1976–2004 pup production estimates. Arrow indicates the large negative residual in 2004.

Even if the rate of increase in pup production has declined, this does not mean that total population size has been similarly affected. A reduction in the rate of increase in total population size will depend on when changes in vital rates occurred over the past 7 yr and on the nature of those changes (*i.e.*, have both survival and birth rate changed). However, to the extent that vital rates are changing in this population, estimates of pup production along with estimates of age-specific birth and mortality rates will be needed to estimate the future size of this gray seal population.

Pinnipeds have several characteristics that argue for extrinsic rather than intrinsic population regulation (Wolff 1997). Two density-dependent factors, which may limit the population, are food and space for parturition and pup rearing. Given that unused habitat is still available on Sable Island and along the coast of eastern Canada and northeastern United States, food is more likely to regulate gray seal numbers, consistent with the general view that most large mammals are regulated by food supply (Sinclair 1996). Between the last estimate of pup production in 1997 and the current estimate, demersal fish biomass on the eastern Scotian Shelf has remained low, whereas the biomass of small pelagic fishes continued to increase (Frank *et al.* 2005). Given the diet of gray seals, conditions favorable to gray seals seem to have persisted; however, the greater number of seals may have resulted in reduced per capita food availability. This is suggested by the marked decrease in odds of being primiparous at age 4 yr in recent cohorts compared to those in the 1980s. Although the mechanism underlying this change in an age of primiparity is unclear, reduced rate of somatic growth resulting from food limitation seems likely (*e.g.*, Bengtson and Laws 1985). However, it is not possible to forecast when food might limit further increase in population size for several reasons. First, we have a poor understanding of the abundance or availability of some of the prey most frequently consumed by gray seals. Second, gray seals are generalist predators (Benoit and Bowen 1990, Bowen *et al.* 1993) enabling them to change diet as prey availability changes. This complicates the estimation of carry capacity, because we have only a rudimentary understanding of the functional response to changes in prey density (*e.g.*, Assenburg *et al.* 2006) or prey preferences that could alter attack rates in ways not predicted solely by prey abundance. Finally, ecosystem changes that have resulted in an increase in the abundance of small pelagic fishes and a reduction in large competitors on the Scotian Shelf (Zwanenburg *et al.* 2002, Frank *et al.* 2005) may have effectively increased gray seal carrying capacity, given that gray seals consume prey that are typically <40 cm long (Bowen and Siniff 1999).

One estimate of pup production lower than expected cannot be considered as strong evidence for a reduction in the rate of population increase. However, when coupled with recent life history data showing a change in the odds of giving birth for the first time at age 4 yr over three successive cohorts, the case becomes more compelling. Nevertheless, more data will be needed to understand the nature of the demography changes occurring in this population.

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APPENDIX

Variance of total pup production was estimated as the sum of the variances for the east and west colonies for the product and quotient of independent random variables (Goodman 1960, Mood *et al.* 1974) as follows:

$$\text{var } N_{ij} = N_{ij}^2 \cdot \left[\left(\frac{g_j}{d \cdot p_i} \right)^2 \left\{ \frac{\text{var}(g_j)}{g_j^2} + \frac{\text{var}(d) \cdot \text{var}(p_i)}{(d \cdot p_i)^2} \right\} \right],$$

where $i = 1$ and 2 for the east and west colony and $j = 1$ and 2 for ground-count corrections for the 12th and 13th, respectively.