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Reduced rate of increase in grey seals at Sable Island: an estimate of 2004 pup production

Réduction du taux d'augmentation de la population de phoques gris de l'île de Sable : estimation de la production de nouveau-nés en 2004

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ABSTRACT

Grey seal pup production on Sable Island, Nova Scotia, has been increasing exponentially since the early 1960s and by 1997 the Sable Island colony was the largest of this species worldwide. Using the same method as in previous years (i.e., an aerial photographic survey), we estimated pup production in January 2004 to determine if this exponential rate of increase in pup production had continued. A total of 33,268 pups was counted on the colour positives. When corrected for the proportion pups seen on the imagery (1.106 for the 12th; 1.527 on the 13th), proportion of pups that died prior to the survey (0.029) 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 = 4380. The 2004 estimate indicates that pup production on Sable Island has continued to increase, but at a reduced rate (r = 0.07 compared to previous 0.128), for almost five decades.

RÉSUMÉ

La production de nouveau-nés chez les phoques gris de l'île de Sable, en Nouvelle-Écosse, a augmenté de façon exponentielle depuis le début des années 1960 et, en 1997, la colonie de l'île de Sable était la plus importante au monde pour cette espèce. En utilisant la même méthode qu'au cours des années précédentes (c.-à-d. un relevé photographique aérien), nous avons estimé la production de nouveau-nés en janvier 2004 pour déterminer si le taux d'augmentation exponentielle de la production de nouveau-nés s'était maintenue. En tout, 33 268 nouveaux-nés ont été comptés sur les positifs couleur. Une fois corrigée en fonction de la proportion de nouveau-nés observés par imagerie (1,106 pour le 12e; 1,527 pour le 13e), de la proportion des petits morts avant le relevé (0,029) et de la proportion des petits nés avant le relevé (colonie de l'est = 0,966, colonie de l'ouest = 0,962), on a estimé la production totale de nouveau-nés à 41 500 individus, avec une erreur-type de 4380. L'estimation de 2004 indique que la production de nouveau-nés à l'île de Sable continue à augmenter, mais à un taux réduit (r = 0,07 comparativement à 0,128 auparavant), depuis pratiquement cinq décennies.

INTRODUCTION

The trend in grey seal (*Halichoerus grypus*) population size at Sable Island, where most pups were born in Eastern Canada, has indicated an exponential increase for the past four decades (Bowen et al. 2003). This sustained increase in pup production, and by inference population size, has resulted in increased grey seal predation, as a result of increased numbers, which may impact marine fish populations of commercial importance in Eastern Canadian (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 continued concern about the sources of mortality, including seal predation, which may be preventing recovery of this stock. The sustained population growth of grey 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. in press).

The grey seal is a generalist predator feeding on a wide range of demersal and small pelagic fishes, but several species tend to dominate the diet seasonally (Bowen and Harrison 1994). Grey seals disperse widely over the continental shelves off eastern Canada and the Gulf of St. Lawrence during the non-breeding season (Stobo *et al.,* 1990; Bowen et al. in press). Within its Canadian range, major grey 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 grey seal pup production at Sable Island. Although pup production has increased over the 7 yr since the last estimate, our results provide the first evidence of a reduction in the rate of increase of pup production. There has also been an increase in age at first birth indicating a change in one vital rate has occurred which is consistent with the reduced rate of population increase.

METHODS

The estimation of pup production follows the approach given in Bowen et al. (1987), Bowen et al. (2003) and Myers and Bowen (1989). The number of pups born up to and including the day of the survey is based on counts of live pups photographed during the aerial survey. This number is then corrected for estimates of the fraction of the following: 1) live pups not detected on the imagery, 2) pups that had died prior to the survey and were not visible on the imagery, and 3) pups that were born after the survey.

As the population increased, more of the island has been used by lactating females, such that in 2004, for the first time, pups were born along the entire length of the island. Thus, in 2004 the entire island was photographed. The photographic survey was conducted using an A-star Helicopter over two days with most of the island photographed on 12 January between 10:09 and 14:09 h (Atlantic Standard time), and the balance photographed on 13 January between 13:43 and 14:21 h. 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 colour-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.

A single experienced reader examined colour positives twice after a period of training on selected photographs and training was continued until consistent counts were achieved. Each 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.

Pup production estimates

Total pup production was estimated as follows:

$$N_{total} = \sum_{i=1}^{2} \sum_{j=1}^{2} \left(\frac{clp_{ij} \bullet gc_j \bullet d}{p_i} \right) \tag{1}$$

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 *clp* is the count of live pups on the positives, p is the proportion born prior to the time of the survey in each stratum, *gc* is the ground-count correction, and d is the proportion that had died up to the day of the photographic survey. We also estimated the number of live pups (N_{live}) by not correcting for the fraction that died prior to the survey. Standard error of total pup production was estimated from the estimated variances of correction factors using the delta method for independent random variables (Mood et al. 1974).

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 west end of the colony.

The proportion of live pups that were photographed but not detected on the positives was determined by comparing pups counts 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. The corners of each plot were demarcated with red vinyl fabric enabling us to locate the plots on the colour positives. The size of the plots varied so that each plot contained > 25 pups. Two ground observers censused 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 changes over time of the proportion of pups in the colony in each developmental stage. Pups were classified into five stages based on a combination of pelage colouration and body shape (Table 1 and 2). 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 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 distribution of births over time. 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 $j+1$:

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

where *s* = 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*.

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

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

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

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

Pup mortality rate

To estimate the fraction of pups that may have died prior to the photographic survey, we regularly (~ every 3d) counted and marked the number of dead pups in nine well-defined areas of the colony. The areas were selected to represent a range of pup densities, but had to be bounded 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 ~ 2 weeks) grey seal pups were hot-iron branded with individual marks during four years in the mid-late 1980s and again from 1998 through 2002. These pups provided a sample of females that could be monitored annually from their first birth.

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. Although some of the females branded on Sable Island as pups may give birth at other colonies, Sable Island is by far the largest colony and therefore we expected that most females would return to Sable Island to give birth for the first time.

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

RESULTS

The single aerial survey conducted over two days yielded a count of 33,268 pups, 6,368 (19.1 %) on 196 positives (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 the January 12th, accounting for the majority of the pups counted (85.6%). The remainder of the pups (i.e., 4,802) was photographed on the January 13th. 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 difficult. Additional light snow fell overnight and January 13th was darker overcast resulting in poorer quality photographs.

Based on ground counts, the 9 ground-control plots contained from 29 to 74 pups (Table 3). 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 on the 13th was poorer on the 13th than on the 12th. The photo-quality effect was also evident in the higher correction factor for the dune edge plot on the Lakeshore (Table 3). Thus, our interpretation of these habitat differences is confounded both by imagery quality and timing of ground counts. However, 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 3).

Distribution of births

The developmental stage of 9,615 pups was recorded along ground transects at 9 sites over a 30-day period (Table 4). Two of these sites were located in the west colony and 7 where located in the east colony. Three models were fitted to estimate the distribution of births over time and from that the proportion of pups born on January 12, the day most pups were photographed (Table 5). We used an estimated date of the first observed birth, December 5 and December 10 for the east and west colonies, respectively, to define the limit of the left tail of the modelled distribution. Alternative, earlier and later start dates had little effect on the model fits (Table 5). All three models appeared to fit the data equally well, but all models did not fit the early season proportions of stages 1 and 2 particularly well or the later season proportions of stage 3 (Fig. 1). There might be several reasons for this result 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 (increasing the rate parameter to 7.0 from 5.46) and increasing the duration of stage 2 (decreasing the rate parameter to 2.5 from 5.25). All models fit the data considerably better suggesting that changes in stage duration could easily account for the initial lack of fit. However, this change in stage duration had only a small effect on our estimate of the proportion born (<4%).

Because the models are not nested, we selected the best model on the basis of the lowest log-likelihood. On that basis, we used the results from the Weibull model to estimate the proportion born in both west and the east colonies.

Total pup production

Estimated N_{total} was 41,500 (SE = 4380) was derived from the raw counts of pups in the positives and correction factors for unborn pups, live-pups missed by the reader, and for pups that had died prior to the survey (Table 6) and were not visible on the imagery (Table 7).

Changes in vital rates

In addition to estimating pup production, we were also able to compare changes in the age at first birth in individually branded females for cohorts born in the 1980s and in the late 1990s. These data show that age at first birth increased from age 4 for the 1985-1989 cohorts to age 5 for the 1998-2000 cohorts (Table 8).

DISCUSSION

The current estimate provides evidence of a reduced rate of increase in grey seal pup production on Sable Island. Fitting an exponential model to the most accurate series of pup cohorts (i.e., 1976 to 1997 tagging censuses) gives a predicted 2004 pup production of 60,900 with 95% confidence limits of 48,200 – 76,900 (Fig. 2). Thus the current estimate is substantially below that predicted if pup production had continued to increase at the observed earlier rate. Rate of increase between 1997 and 2004, calculated as log $[(N_{2004}/N_{1997})/7]$, is estimated at $r = 0.070$ compared to the previous rate of $r = 0.128$.

Sources of error in estimated pup production

Pup counts on 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 lower-quality imagery than that in 1997. Our ground counts indicated that the reader missed 11 % of the pups present on the 12th and 53% on the 13th. We corrected for this source of error using data from ground plots. Second, pups that die before the aerial survey has been conducted will not be counted. On Sable Island, drifting sand soon covers dead pups making them invisible. We corrected for pup mortality by marking and counted the cumulative number of dead pups in selected areas throughout the colony and expressing this as a fraction of lived pups counted on the imagery in those areas. However, our correction is presumably an underestimate of the true mortality rate, because the last count of dead pup in those areas was 5 days before the survey was conducted due to poor weather. Although we monitored the change in the distribution of births broadly throughout the colony, the heterogeneity in the distribution of births may not have captured this source of variability adequately in the estimated SE. Finally, stage durations may have differed somewhat from those measured in 1997. This could have biased our estimates, but the magnitude of the bias would appear to be small (see above).

Trend in pup production

Our results indicate a decrease in the rate of increase of pup production on Sable Island. This is the first evidence of that the rate of increase in this population is less than previously observed. Pinnipeds have several characteristics that argue for extrinsic rather than intrinsic population regulation (Wolff 1997). Two potential density-dependent limiting factors are food and space for parturition and pup rearing. As unused habitat on Sable Island and along the coast of eastern Canada and northeastern United States is still available, food is more likely to regulate grey seal numbers, consistent with the general view that most large mammals are regulated by food supply (Sinclair 1996). The increase in age at first birth to 5 yr from 4 yr is consistent with the early expression of food limitation. However, it is not possible with current information on prey abundance to forecast when food might limit further increase in population size. Grey seals are generalist predators (Benoit and Bowen, 1990; Bowen *et al.,* 1993) enabling them to change diet as prey availability changes. Furthermore, like other pinnipeds, grey seals consume prey that are typically < 40 cm long (Bowen and Siniff, 1999). Thus, ecosystem changes that have been observed resulting 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 benefited grey seals, and delayed population regulation by food limitation.

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Table 1. Developmental stages of grey seal pups.

Stage	Description
1	newborns still wet with birth fluids, pelage yellowish tint, skin in loose folds, locomotion awkward
2	neck well defined, trunk of body cylindrical in shape, pelage white
3	neck and trunk of the body combine to produce a fusiform shape, pelage white to light grey
4	lanugo[a] being shed from any part of the body, excepting the face
5	lanugo completely shed exposing the underlying juvenile pelage or isolated tufts of lanugo < 5 cm diameter still present

[a] white birth pelage

Table 2. Mean stage duration and age (± s.e.) of 22 male and 25 female grey seal pups by developmental stage used to model the distribution of births (from Bowen et al. 2003).

	Duration (d)		Age (d)	
Stage	Male	Female	Male	Female
1	3.4 ± 0.91	3.3 ± 0.90	1.2 ± 0.45	1.2 ± 0.45
2	4.4 ± 1.29	4.8 ± 0.85	5.1 ± 0.92	5.2 ± 0.91
3	12.1 ± 2.77	10.0 ± 2.92	13.3 ± 1.52	12.6 ± 1.35
4	7.0 ± 2.30	8.2 ± 3.20	22.8 ± 2.42	21.7 ± 2.36

Table 3. Number of grey seal pups counted on 9 ground plots (G) and from colour positives (P) of those plots taken on the same day (∆t: time difference between G and P).

				Number of pups counted		
Habitat	Location	Date	∆t (min)	(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	~1d	34	16	2.12
	Long Dune	13/01	~1d	49	28	1.75
	Tern Colony	12/01	65	41	36	1.14
Dune edge	Lakeshore	13/01	~1d	29	24	1.21
	Highground	13/01	~1d	34	33	1.03
	East Light Cut	12/01	49	36	35	1.03
12^{th}				263	237	1.106(0.020)
13^{th}				146	101	1.527(0.250)

Table 4. Number of pups by developmental stage (1-5, see Table 1) counted along ground transects at 9 sites (1-7 east colony; 8-9 west colony) over the course of the birthing season on Sable Island.

Location	Date	Transect	Stage					Total
			1	2	3	4	5	
Long Dune, north beach	12/24/2003	1	54	93	15	0	0	162
	12/31/2003	2	29	92	99	2	0	222
	1/07/2004	3	8	59	149	24	17	257
	1/15/2004	4	1	21	124	64	57	267
	1/21/2004	5	2	6	92	74	78	252
Blowout	12/24/2004	1	23	74	43	0	0	140
	1/01/2004	2	11	72	109	4	3	199
	1/07/2004	3	11	47	116	29	14	217
	1/15/2004	4	3	42	112	67	41	265
	1/21/2004	5	2	8	87	66	63	226
Tern Colony to CWS	12/24/2003	1	26	87	41	1	0	155
	12/31/2003	2	5	67	97	2	2	173
	1/07/2004	3	9	36	132	47	26	250
	1/15/2004	4	2	21	120	53	61	257
	1/21/2004	5	2	9	105	77	86	279
Legal Crossing East-North	12/26/2003	1	12	48	60	1	0	121
	12/31/2003	2	13	51	97	2	1	164
	1/07/2004	3	8	39	108	33	18	206
	1/15/2004	4	2	15	89	46	69	221
	1/21/2004	5	2	2	89	55	89	237
Washover West	12/26/2003	1	23	66	16	0	0	105
	12/31/2003	2	36	102	68	1	0	207
	1/07/2004	3	13	54	139	15	5	226
	1/15/2004	4	3	16	125	41	18	203
	1/21/2004	5	2	15	102	59	38	216
Becks East	12/26/2003	1	18	105	16	0	0	139
	12/31/2003	2	32	89	86	0	0	207
	1/07/2004	3	7	38	133	25	2	205
	1/15/2004	4	4	13	113	65	31	226
	1/21/2004	5	2	5	83	59	77	226

4WW	12/26/2003	1	38	86	29	0	0	153
	12/31/2003	2	18	79	97	1	0	195
	1/07/2004	3	10	19	143	22	3	197
	1/15/2004	4	2	14	132	58	13	219
	1/21/2004	5	0	5	111	69	38	223
West Spit, south	12/27/2003	1	43	63	19	0	0	125
	12/31/2003	2	65	72	25	0	0	162
	1/7/2004	3	36	101	115	4	1	257
	1/15/2004	4	8	41	226	7	4	286
	1/21/2004	5	6	19	156	80	33	294
West Spit, north	12/27/2003	1	31	79	32	0	0	142
	12/31/2003	2	63	122	20	1	1	207
	1/7/2004	3	30	116	128	4	0	278
	1/15/2004	4	13	31	250	23	1	318
	1/21/2004	5	4	12	178	103	33	330
Total								9516

Table 5. Estimates of the proportion of pups born by January 12, 2004 based on three model fits for east colony (sites 1-7) and the west colony (sites 8-9).

First birth date	Colony	Model	Shape	Rate	Proportion born	Log-Likelihood
Early Dec 1	1-7	Log-Logistic	4.05(0.160)	0.039(0.001)	0.883(0.015)	-8883.90
		Gamma	7.09(0.541)	0.272(0.023)	0.934(0.012)	-8865.79
		Weibull	3.23(0.105)	28.05(0.625)	0.975(0.007)	-8861.35
Dec 6	8-9	Log-Logistic	5.24(0.820)	0.039(0.001)	0.878 (0.042)	-2631.28
		Gamma	10.42(2.835)	0.404(0.117)	0.910(0.034)	-2643.56
		Weibull	4.23(0.368)	27.55(0.817)	0.969(0.019)	-2610.69
Mid Dec 5	1-7	Log-Logistic	3.19(0.150)	0.045(0.002)	0.854(0.020)	-8897.49
		Gamma	4.72(0.392)	0.210(0.020)	0.919(0.014)	-8881.24
		Weibull	2.64(0.099)	23.97(0.619)	0.966(0.008)	-8851.18
Dec 10	8-9	Log-Logistic	4.10(0.745)	0.046(0.002)	0.849(0.055)	-2649.62
		Gamma	6.81(2.079)	0.308(0.103)	0.894(0.042)	-2660.63
		Weibull	3.45(0.343)	23.42(0.778)	0.962(0.021)	-2616.77
Late Dec 10	1-7	Log-Logistic	2.07(0.150)	0.054(0.003)	0.771(0.032)	-8963.92
		Gamma	2.42(0.246)	0.129(0.017)	0.881(0.021)	-8943.28
		Weibull	1.86(0.099)	19.08(0.628)	0.937(0.014)	-8900.07
Dec 15	8-9	Log-Logistic	2.61(0.681)	0.056(0.006)	0.762(0.103)	-2709.02
		Gamma	3.27(1.31)	0.179(0.090)	0.843(0.074)	-2714.26
		Weibull	2.41(0.355)	18.31(0.713)	0.938(0.034)	-2664.16

Table 6. Estimates of the fraction of pups that died up to 7 January at 9 sites on Sable Island.

Location	Number dead	Live pups	Proportion dead
Beck's Cove	5	167	0.030
Blowout	33	1268	0.026
CWS	16	549	0.029
East Light, north beach	49	1082	0.045
East Light cut, N	4	238	0.017
Lakeshore	44	1395	0.032
Legal Crossing, E	21	1392	0.015
No. 4 West	13	239	0.054
No. 4	11	311	0.035
Combined	191	6,641	0.031(0.004)

Table 7. Estimate of grey 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 $12^{th}/13^{th}$	6,368/0	22098/4802	
Ground-count correction $12^{th}/13^{th}$	1.106/-	1.106/1.527	
Proportion born 12^{th}	0.962	0.966	
N_{live}	1.031	1.031	
N_{total}	7,555(362)	33,959(4366)	41,500[1](4381)

[1] rounded to the nearest hundred

Table 8. Number and percentage at first birth for ages 4 to 7 yr for cohorts 1985 through 2001.

Cohort		Age (yr) 4	5	6	Total observed
1985	n	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	n	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	n	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	n	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	n	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	n	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	n	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

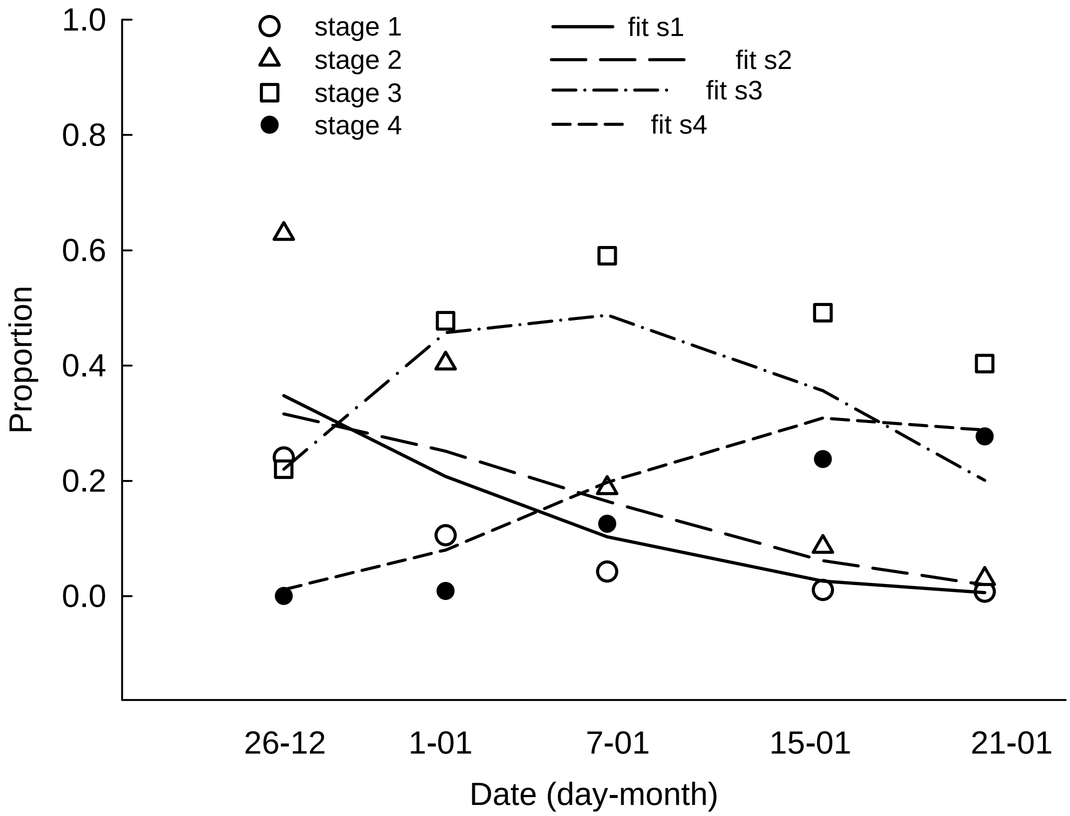

Fig. 1. Observed and model estimates for stages 1-4 in the east colony (Weibull distribution, see Table 7) of the proportion of each pup stage throughout the breeding season in 2004 in the east colony and the west colony.

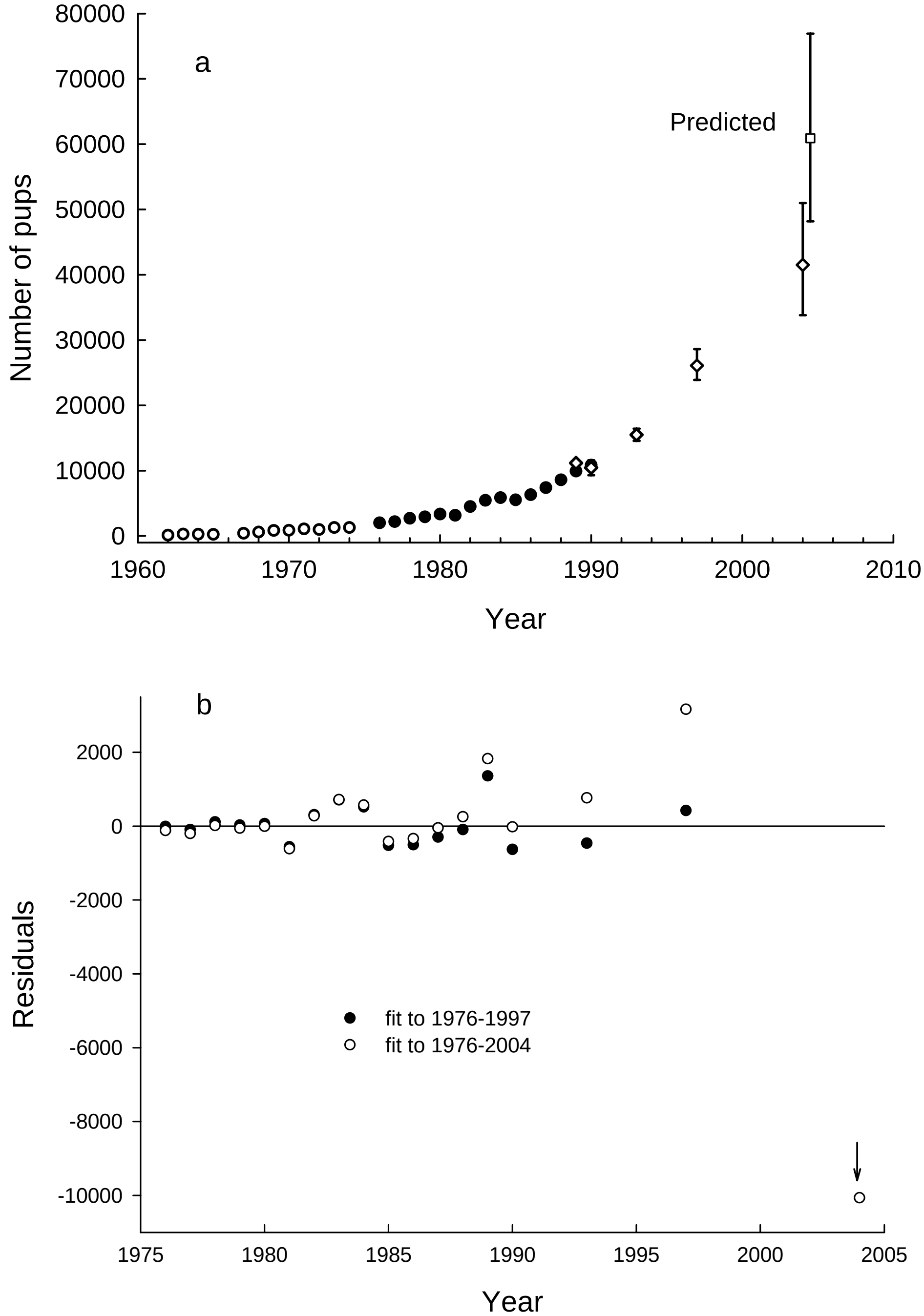

Fig. 2. Trend in grey seal pup production on Sable Island, 1962 to 2004, based on incomplete tagging (1962-1974), complete cohort tagging (1976-1990) and aerial photographic surveys (1989-2004). Error bars are approximate 95% confidence limits. Open square is predicted pup production in 2004 (staggered by 0.5 yr) from an exponential model in Bowen et al. (2003), b) Residuals from exponential fits to the 1976 to 1997 and to the 1976 to 2004 pup production estimates. Arrow indicates the large negative residual in 2004.