

Sustained exponential population growth of grey seals at Sable Island, Nova Scotia

W. D. Bowen, J. McMillan, and R. Mohn

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Grey seal pup production on Sable Island, Nova Scotia, has been monitored since the early 1960s. We estimated pup production on Sable Island in 1997 using aerial photography with a correction for detection of pups on the imagery and a statistical model to account for the proportion of pups not born at the time of the survey. A total of 20 863 pups were counted on the colour positives. When corrected for the proportion of pups seen on the imagery (0.96) and the proportion of pups born before the survey (east colony 0.94, west colony 0.66), estimated total pup production was 25 400 with approximate 95% confidence limits of 23 500 and 26 900. The 1997 estimate indicates that pup production in this population, now the largest grey seal colony in the world, has been increasing exponentially at an annual rate of 12.8% for four decades in the face of considerable environmental variability.

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Introduction

Populations of large, long-lived mammalian carnivores, including pinnipeds, are expected to be relatively persistent in ecological time, though there is little evidence that they fluctuate about some equilibrium value (Harwood and Rohani, 1996). Although the population size of such long-lived species may decline rapidly as a result of exploitation (York and Hartley, 1981), epizootics (Harwood and Hall, 1990; Young, 1994) or rapid environmental changes such as El Niño (Trillmich and Ono, 1991), rates of population increase, in the absence of immigration, are constrained by vital rates. Populations that have been severely reduced may increase exponentially until the rate of increase is slowed by density-dependent factors (Sinclair, 1996). However, there are relatively few examples of this exponential growth phase in pinnipeds and other marine mammals (e.g. northern elephant seals, *Mirounga angustirostris*, Stewart, 1992; Antarctic fur seals, *Arctocephalus gazella*, Payne, 1977; Boyd, 1993). The reasons for this are not difficult to appreciate. As Harwood and Rohani (1996) pointed out, the oceanic life style, long lives, and history of heavy exploitation by man have made it difficult to collect adequate time series of population trends for many species until relatively recently.

The grey seal (*Halichoerus grypus*) is a size-dimorphic member of the family Phocidae, with males being about

20% longer and 50% heavier than females. Most females give birth to a single pup each year, beginning at age of 4 years and continuing for several decades. Grey seals disperse widely over the continental shelf during the non-breeding season (Stobo *et al.*, 1990), but show high levels of philopatry. In the Northwest Atlantic, major 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). Grey seals are currently the most abundant pinniped species on the Scotian Shelf throughout the year and in the Gulf of St. Lawrence during summer and fall.

Historical population trends of grey seals are poorly known. However, bounty hunting and perhaps other factors reduced grey seal numbers in eastern Canada to only a few thousand individuals by the early 1960s (Mansfield and Beck, 1977; Zwanenburg and Bowen, 1990). Since then, the most accurate estimates of grey seal pup production come from Sable Island where most pups were tagged between 1962 and 1990 (Mansfield and Beck, 1977; Stobo and Zwanenburg, 1990). However, numbers on Sable Island prior to 1976 were often based on short visits to the island and as a result pup production was generally underestimated (Zwanenburg and Bowen, 1990; Mohn and

Bowen, 1996). Between 1976 and 1990, censuses were based on tagging all newly weaned pups. These data showed that the trend in pup production was exponential, at an annual rate of increase of about 13% (Zwanenburg and Bowen, 1990; Mohn and Bowen, 1996).

This sustained increase in pup production, and by inference population size, is of interest for two reasons. First, increased grey seal predation mortality may impact marine fish populations of commercial importance in eastern Canada (Mohn and Bowen, 1996; Fu *et al.*, 2001). Second, the sustained population growth provides an opportunity to examine the extent to which the dynamics of a large marine carnivore are linked to long-term changes in marine ecosystems. Here we report on the most recent aerial photographic survey of grey seal pup production on Sable Island, which provides evidence for the continuing exponential growth of this population in the face of considerable environmental variability.

Methods

Photographic survey

The estimation of pup production follows the general approach given in Bowen *et al.* (1987) and Myers and Bowen (1989). The number of pups born prior to the survey is based on counts of pups on aerial photographs. This is then corrected for (1) errors arising from misidentifying the number of pups recorded on the imagery, (2) estimates of the number of pups that had died prior to the survey, and (3) estimates of the number of pups that will be born after the survey (by modelling the distribution of births over time).

A single photographic survey was conducted for the east and west colonies on Sable Island on 15 January 1997 between 11:00 and 16:00 h (local time) using a Piper Turbo Aztec "F" fixed-wing aircraft. The plane was equipped with a radar altimeter and motion compensation camera housing. Photographs were taken with a Jena LMK 15 camera equipped with a 152.163-mm lens, clear filter, and Aviphot Chrome 200 colour-positive film. Pups were born at the east and west ends of Sable Island with a gap of some 10 km between these two areas. A series of parallel transects were flown at the east (18 transects) and west colonies (three transects) at an altitude of 750 feet (231 m) to provide complete photographic coverage of these two areas. 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 once after a period of training on selected photographs. Each positive was examined over a light table using an illuminated hand lens (eight times magnification). The number and position of pups were recorded on a clear acetate overlay by circling images on the positives. A correction for improvement in the identification of pups due to experience was estimated by re-reading 20 positives

from the first roll of film counted after completing all rolls. The 20 positives were selected to represent a wide range of pup densities and habitats.

Pup production estimates

Total pup production was estimated as

$$P_{\text{total}} = \sum_{i=1}^2 (((PC_i \times GC)/B_i) + D_i) \quad (1)$$

where $i = 1$ and 2 for the east and west colonies, respectively, and PC is the count of pups on the positives, B is the fraction born prior to the time of the survey in each stratum, GC is the ground-count correction, and D is the number that had died up to and including the morning of the day of the photographic survey. Confidence limits on total pup production were estimated from the standard errors associated with the proportion of pups born in each colony at the time of the survey and the proportion not visible on the imagery.

The accuracy of the counts from colour positives was determined by locating ground plots on the positives, and comparing counts from the positives 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 blue vinyl enabling us to locate the plots on the colour positives. All plots contained >25 pups. Two observers counted plots independently as close as possible to the time the survey aircraft was overhead. Differences between observers were resolved before going to the next plot. Live and dead pups were counted separately to determine whether the reader could detect dead pups in the imagery.

Temporal distribution of births

Two kinds of information were used to model the temporal distribution of births: 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). These stages were similar to those defined by Radford *et al.* (1978) and Kovacs and Lavigne (1985). To determine stage duration, developmental stage was recorded daily for a sample of pups born on 1 and 4 January 1997 until they had completely moulted (i.e. reached the last stage). On both days, six pups were selected at each of four sites to test the hypothesis that local conditions may affect stage duration. Because one female abandoned her pup after several days, final sample size was 47.

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 eight ground sites (Figure 1). At each site, a researcher recorded

Table 1. Developmental stages of grey seal pups (lanugo: birth pelage).

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 body combine to produce a fusiform shape, pelage white to light grey
4	Lanugo 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

the stage of pups nearest (2–4 m depending on density) to an all-terrain vehicle travelling slowly through the colony along a transect. Mothers and pups typically moved less than a body length on our approach such that avoidance did not bias stage counts. The counts along each ground transect continued until there was a natural break in the spatial distribution of pups. Although at the same nominal site, the location of each transect differed somewhat over the breeding season.

We estimated the temporal distribution of births using the method described in Bowen *et al.* (1987) and Myers and Bowen (1989). However, the integral equations were modified to their discrete analogues with a discrete time step of one day. We assumed a population in which the birth rate in a year can be adequately described by a continuous function of time, $m_j(t)$, which we call the distribution of births over time. The $m_j(t)$ was discretized because pups were counted periodically, not continuously.

Pups pass through a series of identifiable age-dependent stages. 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 $m_j(t)$.

If mortality can be ignored, the rate at which a pup enters successive stages is given by the recurrence relationship:

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

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

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

where s is an index 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 at 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 .

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

Because stage 5 is the final stage during our study, the $[1 - \sum \phi_j(s)]$ 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

$$p_a = \frac{\sum_{j=1}^4 n_j(t_i)}{\sum_{t=0}^{t_i} m_1(t)} \tag{5}$$

Statistical analyses were preformed using SPSS version 10. The standard error (s.e.) is given as a measure of variability about means.

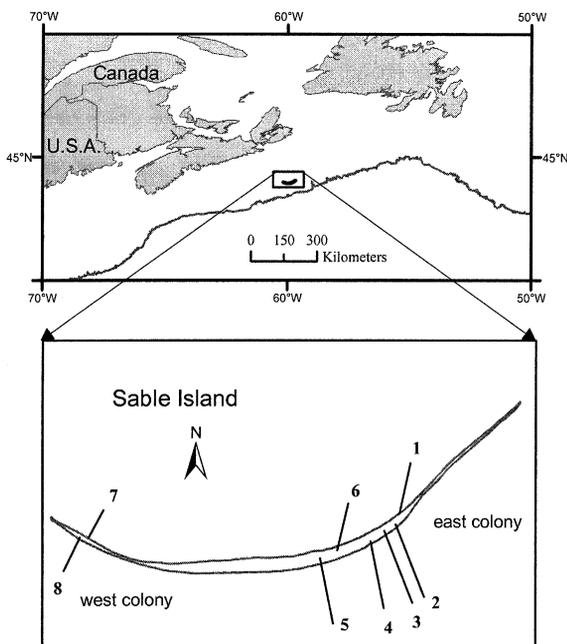


Figure 1. Map showing the location of Sable Island (within the ellipse) and the location of eight ground transects (numbers 1–8) on the Island used to estimate the proportion of pups in each developmental stage over the course of the breeding season.

Results

The single aerial survey yielded a count of 20 863 pups, 3359 (16.1%) on 80 positives of the west colony and 17 504 on 423 positives of the east colony.

Based on ground counts, the nine ground-truthing plots contained from 28 to 81 pups (Table 2). Correction factors (ground count/counts from positives) varied from 0.95 to 1.16 and did not differ by habitat ($F_{2,6} = 4.83$, $p = 0.06$), although correction factors tended to be larger on the dune edge plots. In four cases, ground counts were done within 15 min of when the plots were photographed, in the other five cases 76–105 min had elapsed. Seals did not appear to be disturbed by the survey aircraft. The difference in the correction factors from these two sets was not significant (means = 1.03 and 1.06, respectively; $F_{1,7} = 0.71$, $p = 0.43$).

To determine if reader counts improved with experience, the first 20 photographs (pup numbers ranging from 4 to 380) were re-examined after all the photographs had been read. In 12 cases, the same number of pups were found, in another four one pup less was found, and in the remaining four frames between one and three more pups were found. The mean difference ($0.23 \pm 1.69\%$) did not differ significantly from zero (one-sample t-test, $p = 0.87$). There was no correlation between the relative mean difference and number of pups counted (Spearman's $r = -0.33$, $p = 0.16$). Based on these results, a correction for improvement with experience was considered unnecessary.

Duration of developmental stages

Separate two-way, repeated-measures general linear models (GLM) were used to investigate the effects of location and sex on stage duration and mean age of pups in each stage, with stage as the within subjects effect. Stage duration differed significantly among stages with stage 3 being the

Table 3. Mean stage duration and age (\pm s.e.) of 22 male and 25 female grey seal pups by developmental stage.

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

longest and stage 1 the shortest ($F_{3,117} = 95.5$, $p < .01$, Table 3). Location was not significant ($F_{7,39} = 2.0$, $p = 0.07$) and there was no stage \times location interaction ($F_{21,117} = 1.1$, $p = 0.40$). The effect of sex on mean duration was not significant ($F_{1,45} = 0.4$, $p = 0.54$), but the sex \times stage interaction was significant ($F_{3,135} = 4.6$, $p < 0.01$). Sex had no significant effect on the mean age of pups in each stage ($F_{1,45} = 2.3$, $p = 0.14$). Based on these results, a single stage duration vector was used to model the distribution of births.

Pup production

The developmental stage of 9650 pups was recorded along ground transects at eight sites (Figure 1) over a 30-day period (Table 4). Two of these sites were located in the west colony and six in the east colony. We used general log-linear models to investigate the hypothesis that the distribution of pup stages did not differ among sites sampled at the same time. In this analysis, we used stages 1–3 and the first transect (dates January 1–3) from each of the eight sites. With all eight sites in the model, the hypothesis of homogeneity was rejected (Table 5). In the east colony, sites 1 and 2 were not significantly different from one another, but differed significantly from the other four east sites. Sites 4, 5, and 6 were also similar to one

Table 2. Number of grey seal pups counted on nine ground plots (G) and from colour positives (P) of those plots taken on the same day (Δt : time difference between G and P in minutes).

Habitat	Location	Δt	(G)	(P)	G/P
Sand beach	Tern Colony	105	38	37	1.03
	South Blowout	102	28	26	1.08
	West Washover	12	37	35	1.06
Mean					1.05
Vegetated	Stepple Flat	13	53	53	1.00
	Gully	13	81	80	1.01
	Tern Colony	91	35	37	0.95
Mean					0.99
Dune edge	CWS	76	56	51	1.00
	Handsome Dune	12	31	30	1.03
	East Light Cut	100	44	38	1.16
Mean					1.09
Overall mean (\pm s.e.)					1.05 (\pm 0.02)

Table 4. Number of pups by developmental stages (1–5) counted along ground transects at eight sites (1–6 east colony; 7 and 8 west colony) over the course of the pupping season on Sable Island.

Transect	January date	Pup stage					Total
		1	2	3	4	5	
Long Dune, NB	2	65	115	64	4	0	248
	7	30	94	162	24	2	312
	14	43	53	170	130	21	417
	21	14	35	117	121	132	419
	28	4	13	62	106	157	342
Blowout	2	53	79	47	7	1	187
	7	14	61	112	27	6	220
	14	11	31	98	103	27	270
	22	2	28	78	86	95	289
	28	2	4	46	77	103	232
Washover	2	69	96	5	1	0	171
	7	13	99	91	4	0	207
	14	7	46	166	57	6	282
	22	1	14	75	94	83	267
	28	4	7	31	103	123	268
Legal crossing	03	78	71	24	0	0	173
	07	21	106	68	1	0	196
	14	15	49	157	35	2	258
	22	5	16	98	82	77	278
	28	1	5	49	93	128	276
Beck's Cove, SB	03	78	113	36	1	0	228
	07	33	61	108	6	2	210
	14	24	64	142	74	9	313
	22	10	14	68	81	68	241
	28	6	10	60	83	111	270
#4 West	03	58	73	42	4	0	177
	07	29	84	81	11	0	205
	14	26	50	155	47	12	290
	21	10	19	104	62	68	263
	28	1	12	47	58	84	202
West, north	01	32	14	2	0	0	48
	10	104	151	70	5	0	330
	17	34	77	118	17	2	248
	24	15	20	119	36	13	203
	31	8	12	61	78	47	206
West, south	01	62	50	16	0	0	128
	10	86	92	71	5	0	254
	17	30	54	70	15	2	171
	24	8	20	88	49	20	185
	31	6	10	60	54	36	166
Total							9650

another. The two sites in the west colony (i.e. 7 and 8) did not differ in the number of pups in each stage, but were significantly different from those at the east colony. Given these differences, the distribution of births was modelled separately for the east and west colonies. Heterogeneity within the east colony was ignored, as it was not possible to divide the counts of pups on the imagery into discrete areas based on the estimated heterogeneity.

Table 5. Log-linear test for heterogeneity among sites during the date of the first transect for pup stages 1–3 in 1997 (1–6: east colony; 7 and 8: west colony).

Model	Likelihood	df	p
All sites	101.9	14	0.0001
Sites 1–6	75.5	10	0.0001
Sites 7–8	5.9	2	n.s.
Sites 1–2	0.5	2	n.s.
Sites 1–3	55.4	4	0.0001
Sites 1–4	66.4	6	0.0001
Sites 2–3	42.7	2	0.0001
Sites 3–4	17.8	2	0.0001
Sites 4–5	4.8	2	n.s.
Sites 5–6	4.8	2	n.s.
Sites 4–6	11.7	4	0.02
Sites 6–8	24.9	4	0.0001

Stage duration was modelled using a gamma distribution with different rate parameters and alternating with common shape parameters (five-parameter model) or separate shape parameters (eight-parameter model) for each stage (Table 6). The eight-parameter gamma model did not seem justified (log – likelihood ratio = 0.84). Using a five- and eight-parameter Weibull distribution did not significantly improve the log-likelihood (–646.5 and –642.5, respectively). Therefore, we used the results of the five-parameter gamma model to estimate stage durations.

Three models were fitted to estimate the distribution of births over time and from that the proportion of pups born on January 15 (Table 7). For all models, the date of the first observed birth (December 10 and December 20 for the east and west colonies, respectively) was used to anchor the left tail of the modelled distribution. All three models appeared to fit the data equally well (Figure 2) and predicted that the proportion of pups born prior to the survey was greater in the east colony than in the west colony. 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 the east and the gamma model for the west.

Table 6. Parameters of the gamma distribution fit to pup stage-duration data.

Stage	Common shape, separate rate model		Separate shape, separate rate model	
	Shape	Rate	Shape	Rate
1	21.22	5.46	12.43	4.31
2	21.22	5.25	23.10	5.70
3	21.22	2.02	19.64	1.87
4	21.22	3.01	24.14	3.42
No. of parameters	5		8	
log-likelihood	–642.0		–641.5	

Table 7. Estimates of the proportion of pups born by January 15 (F_{born}) based on three model fits for east colony (sites 1–6 combined) and the west colony (sites 7 and 8 combined), separately.

Colony	Model	Shape (s.e.)	Rate (s.e.)	F_{born} (s.e.)	Log-likelihood
East	Log-logistic	4.04 (0.16)	0.045 (0.001)	0.871 (0.009)	–9747
	Gamma	6.58 (0.59)	0.281 (0.025)	0.907 (0.010)	–9762
	Weibull	2.89 (0.12)	25.58 (0.39)	0.932 (0.010)	–9807
West	Log-logistic	2.95 (0.34)	0.045 (0.003)	0.620 (0.056)	–2408
	Gamma	3.91 (0.83)	0.170 (0.048)	0.660 (0.054)	–2417
	Weibull	2.56 (0.13)	23.23 (0.72)	0.736 (0.030)	–2399

Estimated total production (25 400; 95% confidence limits: 23 500–26 900) 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 and were not visible on the imagery (Table 8).

Discussion

The current estimate provides evidence for a continued exponential increase of grey seal pup production on Sable Island. Fitting an exponential model to the most accurate series of pup cohorts (i.e. 1976–1990 tagging censuses; instantaneous rate of increase, $r = 0.1203 \pm 0.0047$ s.e.) gives a predicted 1997 pup production of 24 900, which is within the confidence interval estimated here (Figure 3). When the 1993 and 1997 aerial survey estimates were included in the model, the estimated annual rate of increase in pup production was 12.8%. This indicates that the annual rate of increase has been nearly constant for more than 25 years. In fact, pup counts from as early as 1962 (Zwanenburg and Bowen, 1990) suggest that this period of exponential increase may cover a period of four decades.

Favourable weather and light conditions during the survey resulted in high-quality imagery. However, total pup production cannot be estimated from these counts alone. Four types of additional information are needed. First, some live-pups may be missed on the positives. Our ground counts indicated that the reader missed 4.5% of the pups present. Similar results (4.3%) were reported in comparisons of ground and print counts of grey seal pups on the Orkney Islands (Wyle and Thompson, 1985). We corrected for this source of error. Second, learning by the reader may result in gradual improvement in the proportion of pups that are identified on each positive. Although this has previously been demonstrated for harp seal pups (Myers and Bowen, 1989; Stenson *et al.*, 1993), there was no evidence of such an effect here. The high-quality, colour imagery and experience of the reader likely accounted for this result. Third, 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 conducting regular censuses throughout the colony. Finally, although we estimated the proportion of pups that were born after the survey was conducted, there is evidence for heterogeneity in the distribution of births within the east colony. With only six sites in this colony, we may not have captured this source of variability adequately in the estimated confidence limits.

The last cohort determined by census (i.e. cohort tagging) was the one born in 1990. Thus, our conclusion that pup production has continued to increase exponentially rests on the comparability of cohort tagging and aerial survey estimates of production. Cohort tagging and aerial surveys were conducted simultaneously on Sable Island in 1989 and 1990 (W. T. Stobo, pers. comm.). Black and white film was used in the 1989 survey, whereas colour-positive film was used in 1990. In both years, the survey was conducted in a manner similar to the 1997 survey with corrections for missed pups and for pups not born at the time of the surveys. The corrected 1989 aerial estimate was 13% higher than the cohort-tagging estimate, whereas the 1990 aerial estimate was 3% lower. However, the confidence limits of the aerial survey estimates included those from cohort tagging, at least for 1990. Of the two calibration surveys, the 1990 survey was more comparable to the 1993 and 1997 surveys because colour film was used in those years. Thus, we have no reason to assume that the corrected aerial survey estimates of pup production differ systematically from those obtained by cohort tagging.

Considering that grey seal pup production on Sable Island has been increasing exponentially for perhaps up to four decades, the question arises when this will end. Populations may be regulated by intrinsic or extrinsic factors. Pinnipeds have several characteristics (females are not territorial; young are not threatened by infanticide; daughters are exposed to unrelated males) that argue for extrinsic rather than intrinsic population regulation (Wolff, 1997). Sinclair (1996) has pointed out that life history traits are adaptations to increase fitness and these traits respond to extrinsic variation. Therefore, intrinsic factors will always be involved in population regulation. Two potential density-dependent limiting factors are food and space for parturition and pup rearing. As unused habitat on Sable

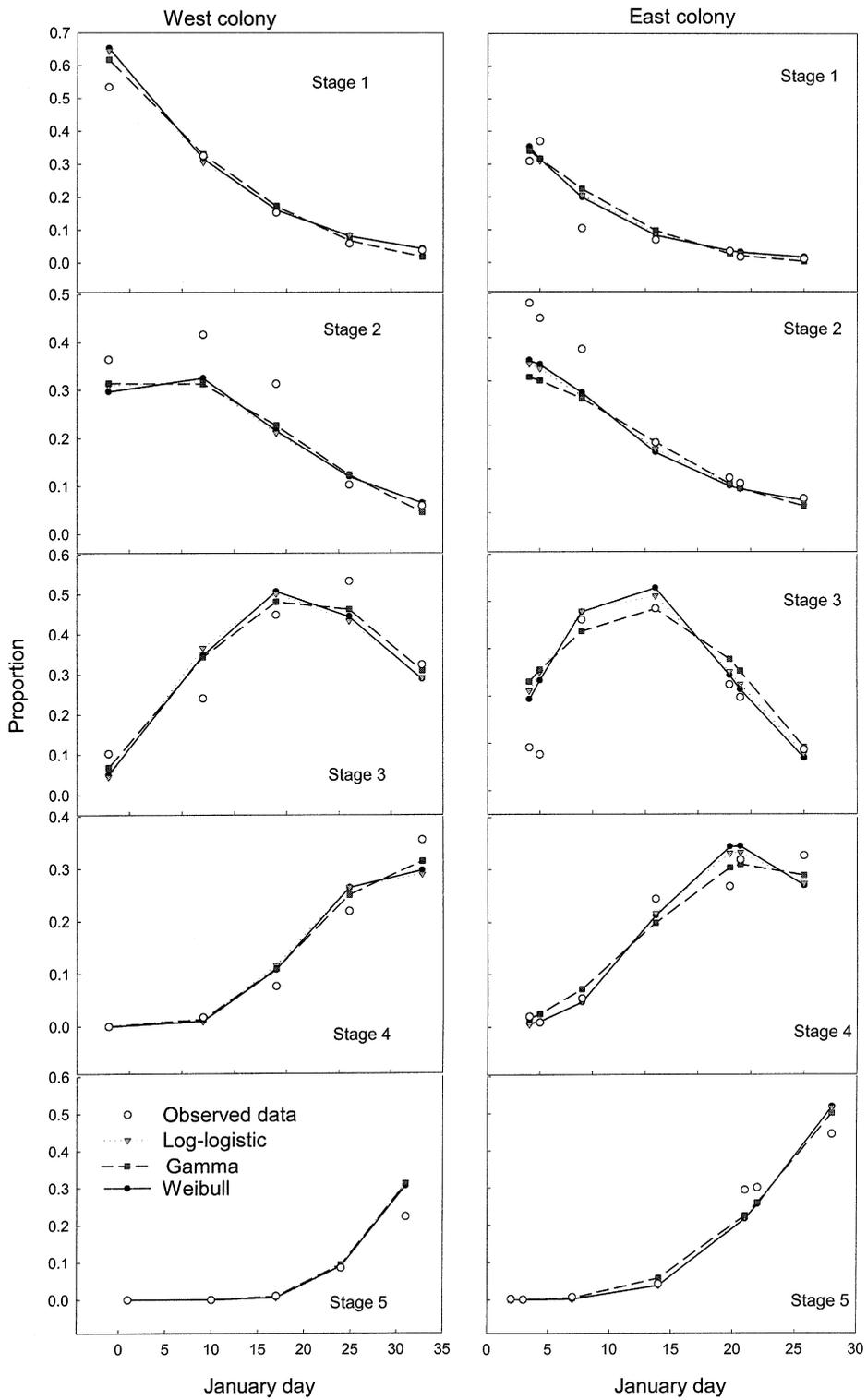


Figure 2. Observed and model estimates (three models, see Table 7) of the proportion of each pup stage throughout the breeding season in 1997 in the east and west colonies.

Table 8. Estimate of grey seal pup production on Sable Island in 1997.

	West colony	East colony	Total
Pup counts from positives	3359	17 504	20 863
Proportion born	0.66 ± 0.05	0.93 ± 0.01	
Ground-count correction	1.05 ± 0.02	1.05 ± 0.02	
Corrected production	5318	19 626	24 944
Dead pups	73	382	455
Total pup production	5391	20 008	25 400 ^a
95% CI	4469–6676	19 046–20 219	23 500–26 900 ^a

^aRounded to the nearest hundred.

Island and along the coast of eastern Canada and northeastern United States is still plentiful, food is more likely to regulate grey seal numbers at some stage, consistent with the general view that most large mammals are regulated by food supply (Sinclair, 1996). However, it is not possible with current information on prey abundance to forecast when food might become limiting.

An interesting feature is that the continued increase in the number of grey seals has occurred in the face of considerable environmental change. Long-term environmental variability of the Scotian Shelf, the marine ecosystem primarily used by grey seals from Sable Island, is summarized in Zwanenburg *et al.* (2002). Interannual variability in water temperature and salinity in this area is among the highest observed in the North Atlantic. On the northeastern Scotian Shelf, the cold intermediate layer water oscillated near or above the long-term mean during the 1960s and 1970s, rose above normal in the early 1980s, fell sharply by the mid-1980s and remained below normal

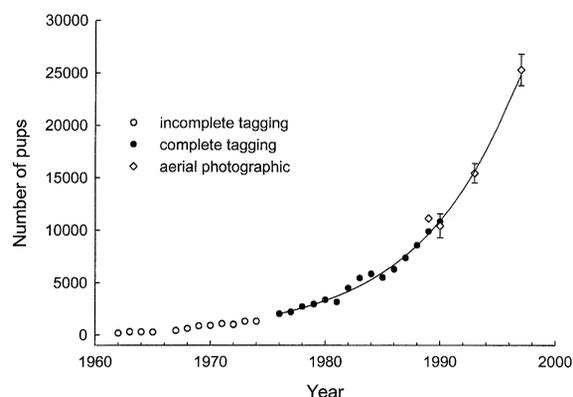


Figure 3. Trend in grey seal pup production on Sable Island, 1962–1997, based on incomplete tagging (1962–1974), complete tagging (1976–1990) and aerial surveys (1989–1997) (error bars: approximate 95% confidence limits; curve: exponential fit to the 1976 through 1990 censuses, see text for equation).

through the 1990s (Petrie and Drinkwater, 1993; Drinkwater *et al.*, 1998). Continuous plankton recorder data of phytoplankton colour index, diatoms, and *Calanus* sp. show significant decadal scale changes between 1961 and 1998 (Sameoto, 2001). The influx of Arctic species is consistent with the colder waters during the 1990s. In addition, a major shift in the phytoplankton production cycle to the earlier months appears to have taken place, with corresponding changes in peak diatom abundance.

Although changes at lower trophic levels are not expected to directly affect grey seal dynamics, bottom-up effects on prey might influence foraging success and hence reproduction and survival. Grey seals consume a variety of small pelagics, flatfishes, and gadoids (Bowen *et al.*, 1993; Bowen and Harrison, 1994). Biomass of demersal fishes on the Scotian Shelf showed a stable to slightly increasing trend through the mid-1980s, but declined precipitously from the mid-1980s to the lowest value observed in the past 30 years. On the eastern shelf, biomass declined by 80% (Zwanenburg *et al.*, 2002). Roughly coincident with marked declines in Atlantic cod (*Gadus morhua*) biomass and colder temperatures on the eastern shelf was a sharp increase in capelin (*Mallotus villosus*) and sand lance (*Ammodytes dubius*) abundance during the late 1980s and through the 1990s (Zwanenburg *et al.*, 2002). Overall, the estimated total fish biomass increased through the 1990s and the average size of demersal fishes declined. Invertebrate abundance also changed with significant increases in snow crab (*Chionocetes opilio*) and shrimp (*Pandalus borealis*) over the same period (Zwanenburg *et al.*, 2002).

In the face of these major marine ecosystem changes, the rate of increase in pup production has remained apparently unaffected. This suggests that both survival and reproductive rates were insensitive to environmental and fishery induced changes. Elsewhere, evidence exists for the effects of environmental variability on the population dynamics of pinnipeds. For example, the collapse of the capelin stock in the Barents Sea in 1985/1987 has been linked to large-scale invasions of harp seals (*Phoca groenlandica*) along the Norwegian coast in 1987. Capelin are an important prey species for the harp seal population, making up more than 90% of the diet in some years. Many of the seals caught in the coastal gillnet fishery were thin and in poor condition (Haug and Nilssen, 1995). Presumably as a result of this large-scale mortality of young seals, the 1986–1988 cohorts were nearly absent (Kjellqwist *et al.*, 1995). Long-term changes in the availability of krill (*Euphausia superba*) have strongly influenced the dynamics of upper trophic-level pinniped and seabird predators in the region of the Antarctic Peninsula (Reid and Croxall, 2001).

In both examples above, predators were dependent largely on a single prey for which a suitable substitution was not available. By contrast, grey seals on the Scotian Shelf are not so dependent on individual prey species (Benoit and Bowen, 1990; Bowen *et al.*, 1993) enabling

them to change diet as prey availability changed. Furthermore, like other pinnipeds, grey seals consume prey that are typically <40 cm long (Bowen and Siniff, 1999). Thus, ecosystem change resulting in an increase in the abundance of small pelagic fishes and a reduction in large competitors may have even benefited grey seals, and delayed population regulation by food limitation.

The continued increase in the grey seal population may have implications for the recovery of depressed fish species, such as Atlantic cod, as it raises the potential for compensatory predation mortality. Predation by grey seals could result in a rapid increase in juvenile mortality on collapsed fish stocks, such as the eastern Scotian Shelf Atlantic cod stock (Fu *et al.*, 2001). This possibility underscores the need to better understand the functional responses of marine mammals to changes in prey abundance.

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