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Analyses of the 1983 Aerial Survey of Harp Seals at the Front:
Corrections for the Birthing Curve and Counting Error

by

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Abstract

We analyze an aerial photographic survey of harp seals (Phoca groenlandica) born off northeastern Newfoundland in March 1983. We estimate the correction to account for pups that had not been born or had left the ice at the time the survey was conducted. We also correct the pup production estimate for negative biases resulting from errors in analyzing the imagery ($\approx 10\%$) and the difficulty of detecting all whelping concentrations (minimum of 10%). Our best aerial survey estimate of production at the Front in 1983 is 295,000 pups. There is reason to believe that this corrected estimate is still negatively biased, however, further correction is not possible with available data. The aerial survey estimate is compared to a mark-recapture estimate also available for 1983.

Résumé

Nous analysons les résultats d'un relevé aérien des phoques du Groenland (Phoca groenlandica) nés au large des côtes nord-est de Terre-Neuve en mars 1983. Nous estimons la correction nécessaire pour inclure les jeunes phoques qui n'étaient pas encore nés ou n'avaient pas encore quitté les glaces au moment du relevé. Nous avons aussi corrigé l'estimation sur la production de jeunes phoques, en raison des biais négatifs résultant des erreurs d'analyse de l'imagerie ($\approx 10\%$) et de la difficulté à détecter toutes les concentrations de nouveaux-nés (minimum de 10%). Notre meilleure estimation de la production, obtenue par relevé aérien, est de 295 000 jeunes phoques en 1983. Nous pensons que cette estimation rectifiée est quand même négativement biaisée, mais que les données disponibles ne permettent pas d'y apporter d'autres corrections. On compare l'estimation dérivée du relevé aérien à une estimation de la recapture des animaux marqués, aussi obtenue en 1983.

Introduction

We present a statistical model that uses population estimates from an aerial survey and information on changes in the proportion age-dependent developmental stages over time to obtain maximum likelihood estimates of total pup production of harp seals (*Phoca groenlandica*) off northeastern Newfoundland (the 'Front'). Like hooded seals, *Cystophora cristata*, (Hay et al. 1985), harp seal pups pass through readily identifiable pelage/morphology stages while on the ice. Therefore, if the distribution of pup stages at several times can be obtained, we can use this information to estimate the birthing ogive and to correct estimates of total population size for pups which are in the water or are yet to be born (see Hay et al. 1985; Myers and Bowen submitted).

The aerial survey we analyze was conducted at the Front in March 1983 by Hay and Wakeham (unpublished manuscript) in conjunction with a mark-recapture experiment conducted both in the Gulf of St. Lawrence and at the Front (Bowen and Sergeant 1985). Hay and Wakeham estimated a pup production of 235,000 in the main two patches, plus an additional 25,000 in a third smaller patch; however, the estimates are negatively biased. Here we estimate the extent of these biases. Both aerial survey and mark-recapture methods have been used to estimate harp seal pup production in the northwest Atlantic (Lavigne et al. 1980; Lavigne 1976; Bowen and Sergeant 1983). Most recent estimates have been from the mark recapture results of tagging conducted from 1978 to 1980. Bowen and Sergeant (1983) noted that although these estimates seemed reasonable in the light of having tested most model assumptions, some assumptions could not be adequately tested to ensure that no bias existed. Therefore, they urged that as many independent methods as possible be used to estimate pup production.

Here we systematically examine sources of bias in aerial surveys of Harp seals. These sources of bias are caused by birthing not being completed at the time of the survey, pups entering the water, pups hidden on the ice, errors in reading aerial photographs, detection of all whelping concentrations, and pups born outside the whelping concentrations. The simultaneous use of aerial survey and mark-recapture methods in March 1983 at the Front, therefore, provides the first opportunity to compare recent mark-recapture results with those from an independent method.

Methods

Pelage Stages

Pelage stage was recorded for most pups that were tagged during the March 1983 mark-recapture experiment described by Bowen and Sergeant (1985). We used the age-dependent pelage/morphometric stages given in Stewart and Lavigne (1980), namely: newborn (1), yellow (2), thin white (3), fat white (4), grey (5), ragged (6), and beater (7).

Pup stages were censused in areas distributed throughout both main whelping concentrations by the use of a helicopters. For logistic reasons, cluster sampling was used rather than simple random sampling of pelage stages.

Cluster size varied from 156 to 442 in the north patch and from 55 to 372 in the south patch. Within each cluster, three or four researchers walked separate transects and classified every pup encountered.

Duration of Pelage Stages

To determine the duration of pelage stages, 10 pups tagged as newborns and 44 pups tagged as yellow coats were resighted as time and weather permitted. At each resighting, the pelage stage of these known age pups was recorded. Of the 54 pups studied, 50 were born and observed in the Gulf of St. Lawrence and 4 were from the Front area.

Aerial Survey Method

The survey was conducted using a Cessna 402 aircraft, equipped with a radar altimeter and VLF-Omega navigation, at an altitude of 152 m. Vertical photographs were taken using a Wild RC-10 camera and Kodak Double-X aerographic black and white film. Once located, a series of systematic continuous-photograph transects were flown throughout the entire patch. An intervalometer was used to obtain 20% overlap between successive photographs. An estimate of the number of pups on the ice at the time of the survey was calculated using a strip survey method for unequal-sized sampling units, as described by Caughley (1977 p. 31) and Norton-Griffiths (1975). Details of the survey method are described in Hay and Wakeham (unpublished manuscript).

Analysis of the Photographs

Before the photographs were examined, an experiment was performed to assess the consistency with which pups were identified by a single reader. For this purpose, 10 representative photographs were selected from the total of 650 photographs taken. Each experimental photograph was examined five times in blind replicates using a 16-cell and a 64-cell acetate grid to test the effect of grid size on consistency. Thus, each experimental photograph was examined five times with each grid for a total of 10 readings per photograph. An 8X illuminated hand lens was used to examine all photographs.

The 650 photographs were then examined using the 64-cell acetate grid. Each pup was circled on a clean sheet of acetate to form a permanent record of the examination. Photographs were examined once only and were read in sequence from 1 to 650 over a period of about three months by the same reader.

After the general reading of the photographs had been completed, the 10 experimental photographs were reread an additional five times to test the consistency of the reader.

The Model

Consider a population in which the number of animals born in a year can be adequately approximated by a continuous function of time, $m_0(t)$ (see Table 1 for definition of symbols). The species is assumed to pass through a series of identifiable age-dependent stages. Stages are denoted by the subscript j , and

if an animal survives it passes from stage j to $j + 1$. We specify stage duration in terms of instantaneous transition intensity functions

$$\phi_j(\tau) = \lim_{\Delta\tau \rightarrow 0} \left\{ \text{Probability an animal passes from stage } j \text{ to } j + 1 \text{ in the interval } (\tau, \tau + \Delta\tau) \right\} / \Delta\tau,$$

where τ is the time spent in the stage j . This specifies the force of transition into stage $j + 1$ from stage j given the animal has spent time τ in stage j (and has survived). We assume that stage duration is a semi-Markov process, i.e. the transition intensities depend only on the current state and the time so far spent in that stage. For a similar development for an insect population see Ashford et al. (1970).

The number of individuals that enter stage j at time t is denoted by $m_j(t)$. If the rate pups leave the ice is constant and equal to μ , then the m_j 's are connected by the recurrence relationship

$$m_j(t) = \int_0^\infty \exp(-\mu(t-\tau)) m_{j-1}(t-\tau) \phi_{j-1}(\tau) d\tau. \quad (1)$$

The total number of pups in stage j on the ice at time t , $n_j(t)$, is

$$n_j(t) = \int_0^\infty \exp(-\mu(t-\tau)) m_j(t-\tau) \left(1 - \int_0^\tau \phi_j(s) ds\right) d\tau. \quad (2)$$

In general μ will not be held constant in the model but will depend upon stage and the time the pup has spent in each stage.

Natural mortality for harp seal pups from birth to weaning is low (1.1-1.4%, Kovacs et al. 1985; 0.34%, Bowen unpublished data) and will be ignored in this analysis.

We now consider the errors in estimating stage composition. Let S_{ij} be the number of individuals observed to be of stage j at time t_i . The predicted proportions of each stage present on each day, P_{ij} , are calculated as

$$P_{ij} = \frac{n_j(t_i)}{\sum_j n_j(t_i)}, \quad (4)$$

where the $n_j(t_i)$'s are given by (2). If the S_{ij} 's are obtained by taking a simple random sample of the population and determining the stage class of each

individual, then the likelihood function for the P_{ij} 's, is equal to a constant times

$$\prod_{ij} P_{ij}^{S_{ij}} . \quad (5)$$

However, the data on state composition are not simple random samples; they were obtained by cluster samples of a spatially heterogeneous population of pups. This will effect the confidence limits of our estimates, but not our parameter estimates as long the likelihood remains proportional to (5).

Statistical Distributions

We shall use several statistical distributions in our analysis. For these distributions, Greek letters will be used to denote adjustable parameters; ρ always has the dimensions of the reciprocal of time and can be interpreted as a rate, whereas κ is a dimensionless parameter that can be interpreted as 'shape'. The density functions of the distribution used here are

Distribution	Density function
Exponential	$\rho e^{-\rho t}$
Gamma	$\frac{\rho(\rho t)^{\kappa-1} e^{-\rho t}}{\Gamma(\kappa)}$
Weibull	$\kappa \rho (\rho t)^{\kappa-1} \exp[-(\rho t)^\kappa]$
Log logistic	$\kappa \rho^\kappa t^{\kappa-1} [1 + (t\rho)^\kappa]^{-2}$.

Note that the Gamma and the Weibull distribution reduces to the exponential distribution when $\kappa = 1$. Consult Johnson and Kotz (1970), Kalbfleisch and Prentice (1980), and Cox and Oakes (1984) for information on applications of these distributions.

Duration of Pup Stages

Harp seal pups were classified into readily identifiable developmental stages based on observations of pups whose ages were approximately known. Ten pups were individually marked in stage 1, the newborn stage and 44 pups were marked in stage 2, the 'yellow' stage (Table 2). The duration of the newborn stage was independently estimated by watching pups from birth; the resulting estimate of the duration of this stage is six hours (Kit Kovacs, Department of Biology, Guelph University, Guelph, Ontario, pers. comm.). There is insufficient information to estimate the duration of the 'yellow' stage accurately; however it is probably between 12 and 36 hours duration based on the data in Table 2. We assume for simplicity that the duration of the combined newborn and yellow pelage stages is one day for all animals.

The initial age of the marked pups is not known with certainty and the time of resightings is known only to the closest day. To facilitate analysis

of stage durations we make the simplifying assumptions that all pups tagged as newborns were born at noon on the day of tagging, all pups as yellow were born on noon the day before tagging, and that all resightings take place at noon. Thus, the data on resightings of pups that were initially yellow in Table 2 should be shifted to the right one day.

The length of the ragged jacket stage cannot be estimated from the data in Table 2. We shall thus combine the data on ragged jacket and beater seals in the subsequent analysis.

The transition intensity, ϕ_j , of stages 3, 4, and 5 was assumed to be a gamma distribution. Let the proportion of the known-age population in stage j i days after the end of stage 1 be q_{ij} . For any particular parameter values of the gamma distribution the proportion, q_{ij} , can be calculated by setting m_0 to 1 and iterating equations 1 and 2. The likelihood of any combination of parameters is proportional to:

$$\prod_{j=2}^6 \prod_{i=1}^{26} q_{ij}^{N_{ij}} \quad (6)$$

where N_{ij} is the observed number of known-age pups in stage j , i days after the end of stage 1.

Results

Aerial Survey

Estimates of the number of pups in the main Front patches on 17 March from Hay and Wakeham (unpublished data) are:

	Mean	Lower 95% confidence interval	Upper 95% confidence interval
North patch	104,000	47,000	161,000
South patch	129,000	28,000	229,000
Combined	235,000	137,000	334,000.

A third patch was located but could not be photographed on 19 March (50°35'N, 54°15'W). A rough estimate was made of the numbers in this patch by determining its area and by comparing density with density measured in past years; the resulting estimate is between 20,000 and 30,000 pups in this patch.

Counting Errors

We analyzed three types of counting errors: errors during the beginning of the counting of the photographs attributable to a learning process, errors

attributable to the fact that each photograph was read only once (more seals were detected upon multiple readings), and falsely identifying patches of ice as seals.

Evidence of a learning process bias is clear from the data collected on the 10 experimental photographs (Fig. 1, Appendix 1). There is no apparent effect of grid size. If the relationship in Fig. 1 can be extrapolated to the general survey readings, then the reader would have begun the survey readings by missing approximately 25% of the pups he would have seen at the end of the survey, but this effect would become very small after 150 to 200 photographs were read (about one-third of the way through the survey). This would suggest that the undercounting caused by the learning process resulted in an underestimate of about 5%.

We estimated the degree of negative bias attributable to the fact that only one examination was made of each photograph by comparing the readings of the 10 experimental photographs during the last two-thirds of the survey reading with the number of seals identified by combining all readings in Appendix 1 (Table 3); we thus estimate that there is a negative bias from this source of about 4.3%.

It is possible that patches of shaded ice were falsely identified as pups when photographs were examined. We examined this possibility by identifying those pups on the 10 experimental photographs that were not unambiguously seal pups, e.g. flippers were not clearly visible. The proportion of possible false identifications was small - 1.95%.

Duration of Pup Stage

Because our observations were relatively widely spaced, it did not seem justified to fit three independent gamma distributions for stages 3, 4, and 5 to the data in Table 2. We made the assumption that the shape of the transition intensity function was the same for stages, but the scale parameter, ρ , was different for each stage. The resulting estimates obtained by maximizing the likelihood (Eq. 6) are

thin white	$\hat{\rho}_t = 0.431$
fat white	$\hat{\rho}_t = 0.302$
grey	$\hat{\rho}_t = 0.584$
shape parameter (common to all)	$\hat{\kappa}_t = 12.7$

The resulting fit to the data was good (Fig. 2). A 6-parameter model, separate κ_t 's for each stage, was not judged justified by a log-likelihood ratio test, i.e. the ratio of the maximum log-likelihood of the 6- and 4-parameter models was less than 2 (Kendall and Stuart 1979).

Estimating Birthing Distribution

Four quantitative properties of the data were observed:

- 1) The peak day of pupping in the south patch occurs before the first observation on March 10.
- 2) There is no evidence of any pupping more than three days before the first observation.
- 3) Pupping continues for at least 15 days after peak pupping.
- 4) Peak pupping in the north patch is one or two days later than peak pupping in the south patch.

The first three points above imply that the distribution of births over time should be described by a right skewed probability distribution. The log-logistic distribution is used here to describe the distribution of births because it is relatively more skew than other commonly used distributions, e.g. the gamma or log-normal, and its density and distribution functions are easily computed (Kalbfleisch and Prentice 1980; Cox and Oakes 1984). It is necessary to compute the beginning of the distribution, i.e. the time before which no pups are born. Since the shape of the probability distributions are not very sensitive to the choice of a beginning point (Kalbfleisch and Prentice 1980; Johnson and Kotz 1970), we will use the reasonable time of March 7 and test the sensitivity of the results to this assumption.

There is insufficient information to compute a separate birthing distribution for the north patch. We shall therefore combine the data from both patches in the analysis.

As pups age they spend more time in the water, and are thus not observable using air photography. There is unfortunately no quantitative information on changes in the numbers of seals in the water as a function of age. However, we can use the information in Table 3 to estimate this. The approach taken here is to model this process using a distribution sufficiently general to describe a wide range of possible behaviors. It is reasonable to limit attention to distributions where the age-specific rate at which pups entering the water is monotone increasing, decreasing, or constant with age. A useful distribution to describe such behavior is the Weibull distribution which has significant computational advantages over similar distributions such as the gamma. If the parameter $\kappa_\lambda = 1$ the Weibull distribution reduces to the exponential distribution, i.e. the rate pups enter the water is constant. If $\kappa_\lambda < 1$, then the rate at which pups enter the water is monotone decreasing with age and if $\kappa_\lambda > 1$, then it is monotone increasing.

Five models were fit to the data in Table 4. In each model it is clear that peak pupping is predicted to be between March 7 and March 8 (Table 5). The date of first pupping is probably closer to March 7 than March 6, as judged by the maximum-likelihood value of model 2. Between two and three percent of the pups are predicted to be born after the date of the aerial survey March 17.

If pups only begin to enter the water by the grey stage then very few of the pups will be missed by the aerial survey because they have entered the water. However, if 10% of the grey stage are in the water by March 17 then the aerial survey would underestimate the total pup production in the patch by 6%. The shape of the distribution describing the rate at which the ragged jacket stage entered the water had little effect on the estimates, i.e. the results from model 4 and 5 were similar to the results from model 1.

Discussion

The durations of the fat white, grey, and ragged pelage stages are reasonably estimated using the available resighting data from known-age pups. However, sufficient information was not available to estimate separately the durations of the newborn, yellow, or thin white stages and hence an estimate of the combined duration of these stages was calculated. These data, coupled with estimates of the distribution of pelage types within the two major whelping patches over time, show that most pups are born over a period of several days with a peak on 7 March (Fig. 3). There is evidence that pups in the southern patch are born several days earlier than those in the northern patch; however, we did not have enough samples to estimate separate birthing curves for each concentration.

By 17 March when the aerial survey was conducted only a small correction of about 3% was necessary to account for pups which had left the ice or were yet to be born. It is clear from Fig. 2 that surveys conducted between about 12 and 20 March at the Front will not require large correction for the birthing curve. The major uncertainty in this estimate is the uncertain number of seals in each stage that are in the water and are thus not detected by the photographs.

However, accounting for pups which have entered the water or for those yet to be born is only one of a number of factors which will tend to underestimate pup production from aerial surveys (Table 6). Pups hidden from the camera by rafted ice may underestimate production at the Front by 10% according to Lavigne et al. (1980). Although, we have no quantitative estimate of the proportion of pups which may have been hidden from the camera in March 1983, observations by researchers on the ice in March 1983 suggest that the proportion hidden was less than the 10% estimated by Lavigne et al. (1980); perhaps on the order of 3%.

Analysis of the photographs may lead to four sources of error, three of which will result in negative bias (Table 6). First, some pups in the photographs may not be detected by the reader. We have no measure of the magnitude of this error, but given the high quality of the imagery we would not expect this to be a serious problem. Second, there may be improved detection of pups as a result of learning on the part of the reader. Available data suggest that this may have resulted in about 5% underestimation in the 1983 aerial survey. Third, a further increase of about 4% in the number of pups counted would have resulted from multiple readings of each photograph. Finally, false identification of pups would lead to a positive bias; however, this will be small (< 2%). Thus, the estimate of pup production on 17 March of

pups in the main whelping patch was probably negatively biased by 10 to 20% (Table 6).

A major source of underestimation can result from failing to detect all whelping patches (Table 6). In 1983 we know of one patch that was not photographed and there may have been others since a thorough search of ice suitable for whelping was not conducted. The unphotographed patch comprised about 20,000 to 30,000 pups (K. Hay, pers. comm) or about 10% of estimated Front production. Another example of an initially undetected whelping patch occurred in 1980 at the Front. In this case, a large whelping concentration was reported by Rowsell (1980) about 50 mi (80 km) northeast of the 'northern' patch. This patch, discovered during the rescue of a German seaman, had not been located during searching flights of fixed-wing aircraft and thus would have gone undetected. These observations raise doubts about our ability to locate all major whelping concentrations.

Finally, no estimate of production outside of whelping patches was possible with available data. It is generally believed that few pups are born outside of patches, but this belief has not been carefully tested. Our impressions come from sighting surveys conducted at the Front and in the Gulf of St. Lawrence over many years. But single pups could easily be overlooked in such surveys, particularly if the mother was not on the ice, as is often the case. Future surveys should attempt to estimate production outside of concentrations, perhaps by using spot-photographs taken along search transects as was done in our hooded seal work (Hay et al. 1985).

Our best estimate of Front production from aerial survey is 270,000¹ pups plus about 25,000 pups in the unphotographed patch for a total of 295,000, with nominal 95% confidence limits of 184,000 and 405,000. As suggested above, this estimate is more likely to be an underestimate of production than an overestimate, even when corrected for the birthing ogive and counting errors.

How does this aerial survey estimate compare with that from the mark-recapture results for 1983? Direct comparison is difficult because the mark-recapture estimate represents total production, i.e. Front and Gulf, whereas the aerial survey estimate is for Front production only. An approximate estimate of Front production can be calculated using only recaptures of Front-tagged pups recovered during the beater hunt at the Front. This approach will tend to overestimate Front production to some extent because some Gulf-born pups will have migrated to the Front area. Of 367 recaptures of Gulf-tagged pups, 26 or 7% were taken at the Front (Bowen and Sergeant 1985). Estimated production using Front tags alone is 405,000 with nominal 95% confidence limits of 351,000 and 459,000. This estimate is about 37% greater than that indicated from the aerial survey, although there is considerable overlap in the confidence regions of the two estimates. Therefore, given the tendency of aerial surveys to be negatively biased and the wide confidence limits associated with the present aerial survey estimate, it seems unlikely that the mark-recapture results have significantly overestimated pup production on the Front in 1983.

¹235,000 (from survey x 1.15 (correction for 1 to 3, Table 6)).

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Table 1. Symbols used.

$m_0(t)$	= Number of pups born at time t
$m_j(t)$	= Number of pups entering stage j at time t
i	= Time index
j	= Index for the stage class
$n_i(t)$	= Number of pups in stage i on the ice at time t
P_{ij}	= The proportion of pups at time i which belong to stage j
S_{ij}	= The number of pups at time i found to be of stage j
ρ_b	= Rate parameter of birthing distribution
ρ_t	= Rate parameter of transition intensity function for pup stages
ρ_l	= Rate parameter for distribution of stage 6 pups leaving ice
κ_b	= Shape parameter of birthing distribution
κ_t	= Shape parameter of transition intensity function for pup stages
κ_l	= Shape parameter for distribution of stage 6 pups leaving ice

Table 3. Readings of 10 experimental photographs.

Photograph number	Readings during survey	Readings from master sheet
1	55	55
2	103	103
3	99	104
4	46	49
5	155	161
6	74	80
7	63	67
8	60	66
9	94	96
10	89	93
Column mean	83.8	87.4

Table 4. Changes in the observed pelage type for Harp seal pups in March 1983.

Mark pelage	Day									
	10	11	14	15	16	17	18	19	25	28
South patch										
Yellow	15	5	2				1	0	1	0
Thin white	326	50	54				25	3	3	0
Fat white	1	0	224				353	19	27	0
Grey	0	0	11				1005	858	289	8
Ragged	0	0	0				15	30	51	107
Beater	0	0	0				0	0	1	9
North patch										
Yellow				12	12	22				
Thin white				431	545	390				
Fat white				503	1018	1332				
Grey				6	0	14				
Ragged				0	5	12				
Beater				0	0	0				

Table 5. Results for the model of the birthing distribution.

Model	Assumption			Results					
	Date of first pupping	% grey stage visible	Rate stage 6 seals leave ice	Log-logistic parameters of birthing distributions ($\hat{\rho}_b$) ($\hat{\kappa}_b$)		Rate 6th stage leaves ice ($\hat{\rho}_l$)	% on ice at 17 March	% born by 17 March	Log-likelihood (from Eq. 6)
1	March 7	100	Constant	1.17	1.50	0.0154	0.973	0.975	-6497.
2	March 6	100	Constant	0.513	2.68	0.0159	0.99	0.99	-6522.
3	March 7	90	Constant	1.32	1.37	0.0173	0.94	0.97	-6511.
4	March 7	100	Increasing with age ($\kappa_l = 1.5$)	1.15	1.53	0.0276	0.975	0.977	-6483.
5	March 7	100	Decreasing with age ($\kappa_l = 0.5$)	1.17	1.50	0.0022	0.973	0.975	-6499.

Table 6. Sources of bias in the estimation of total numbers from the aerial survey of 17 March.

Source	Magnitude of bias (%)
1. Birthing curve	
a) pups not yet born	-1.0 to -2.5
b) pups in water	0.0 to -5.0
2. Hidden pups on ice not available to the camera	-10.0 (Lavigne et al. 1980, probably less on 17 March 1983)
3. Reading photographs	
a) pups available to imagery but not detected	- ?
b) improved detection of pups (learning)	- 5 to -?
c) single examination	- 4.3
d) False identification of pups	0.0 to 1.95
4. Detection of concentrations	- 10 to -?
5. Low density scattered pups	- ?

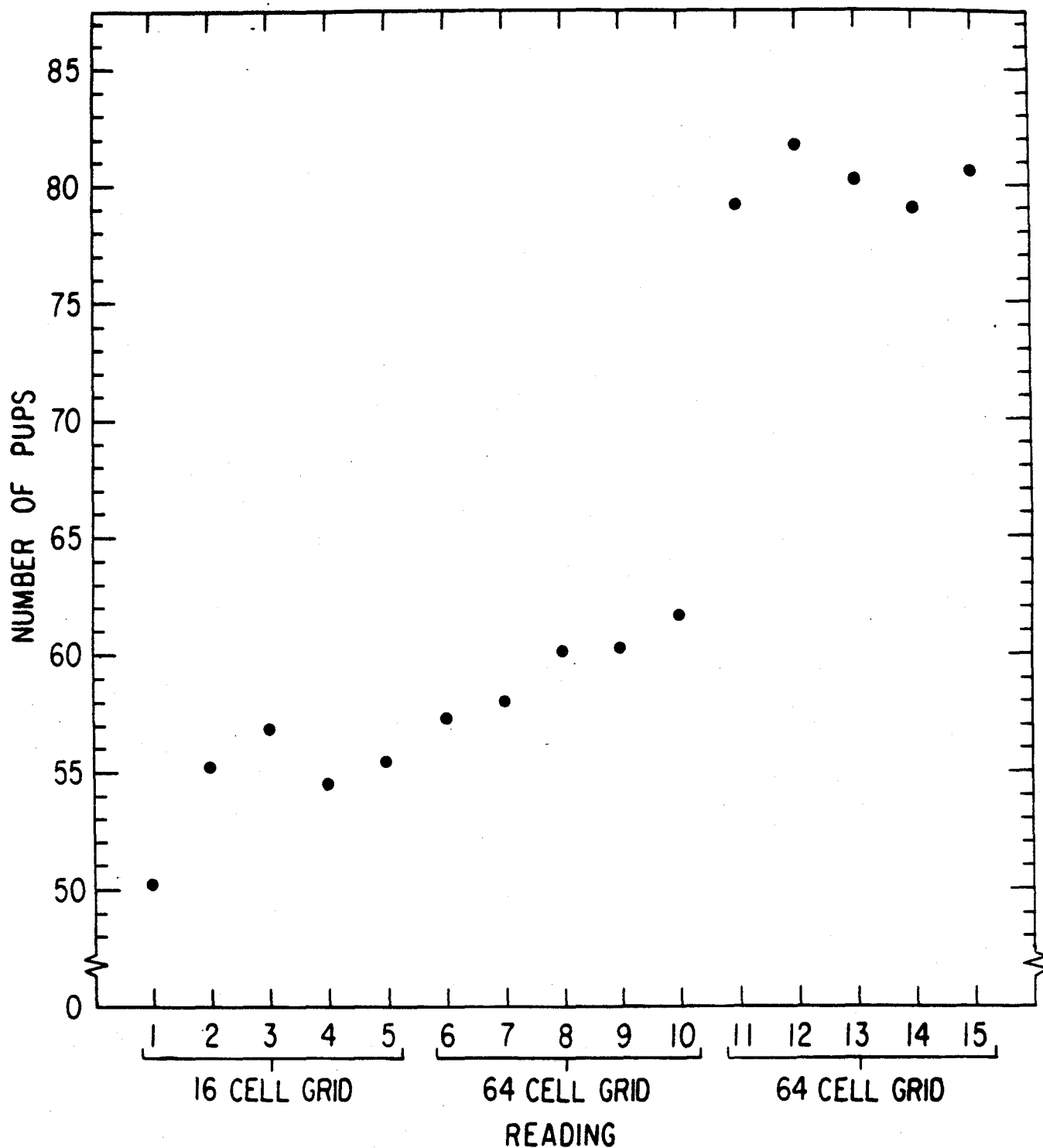
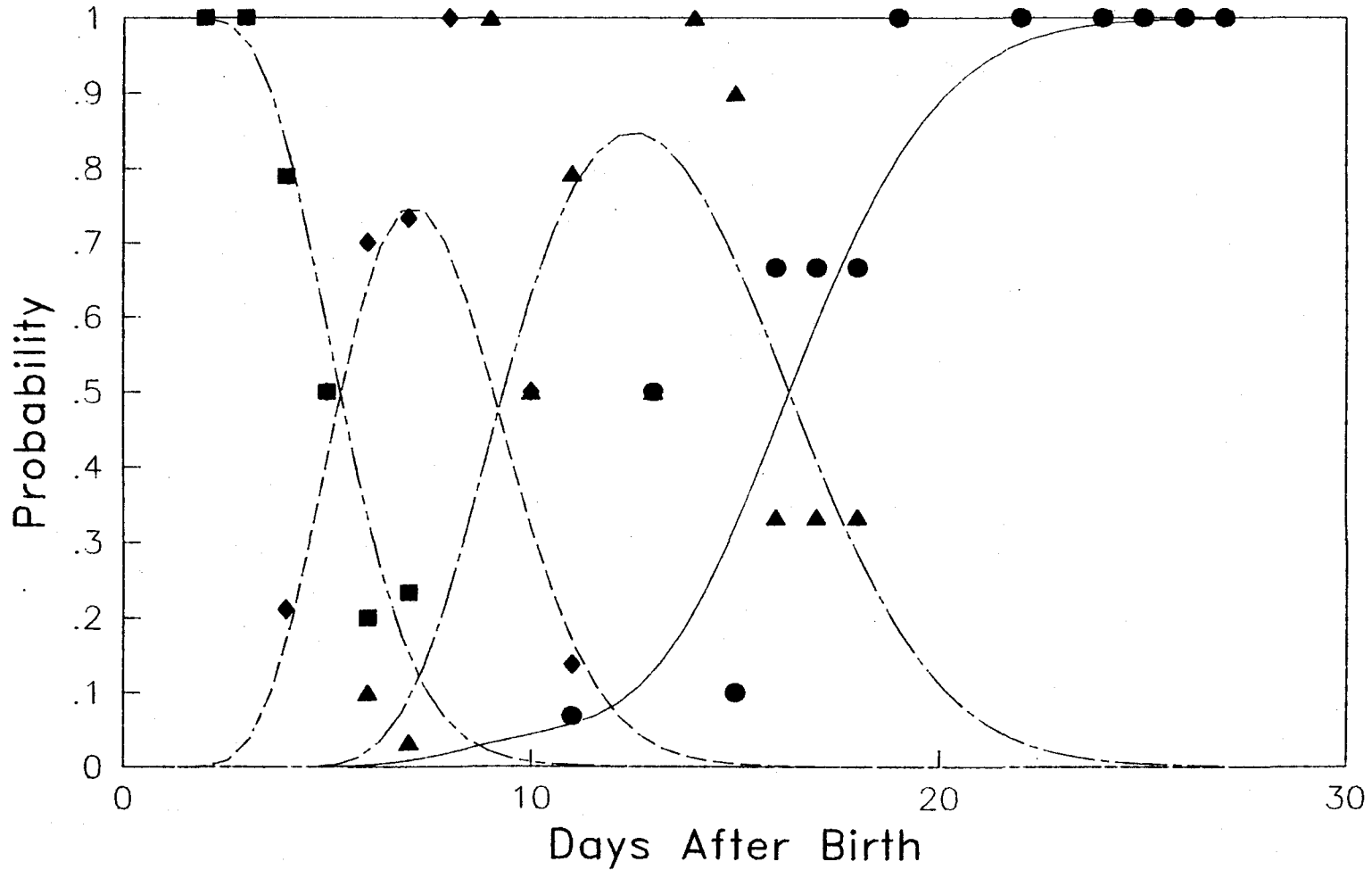


Fig. 1. Mean counts of seal pups from the 10 experimental photographs. The first 10 readings were before the survey photographs were read; they are plotted in the order they were read. The last five readings took place after the survey readings were completed.

Fig. 2. Predicted transition of pups through peltage types based upon data in Table 2. [a. newborn, yellow, plus thin white stage, predicted (---), observed (■); b. fat white stage, predicted (---), observed (◆); c. grey stage, predicted (---), observed (▲); d. ragged jacket plus beater stage, predicted (—), observed (●).]



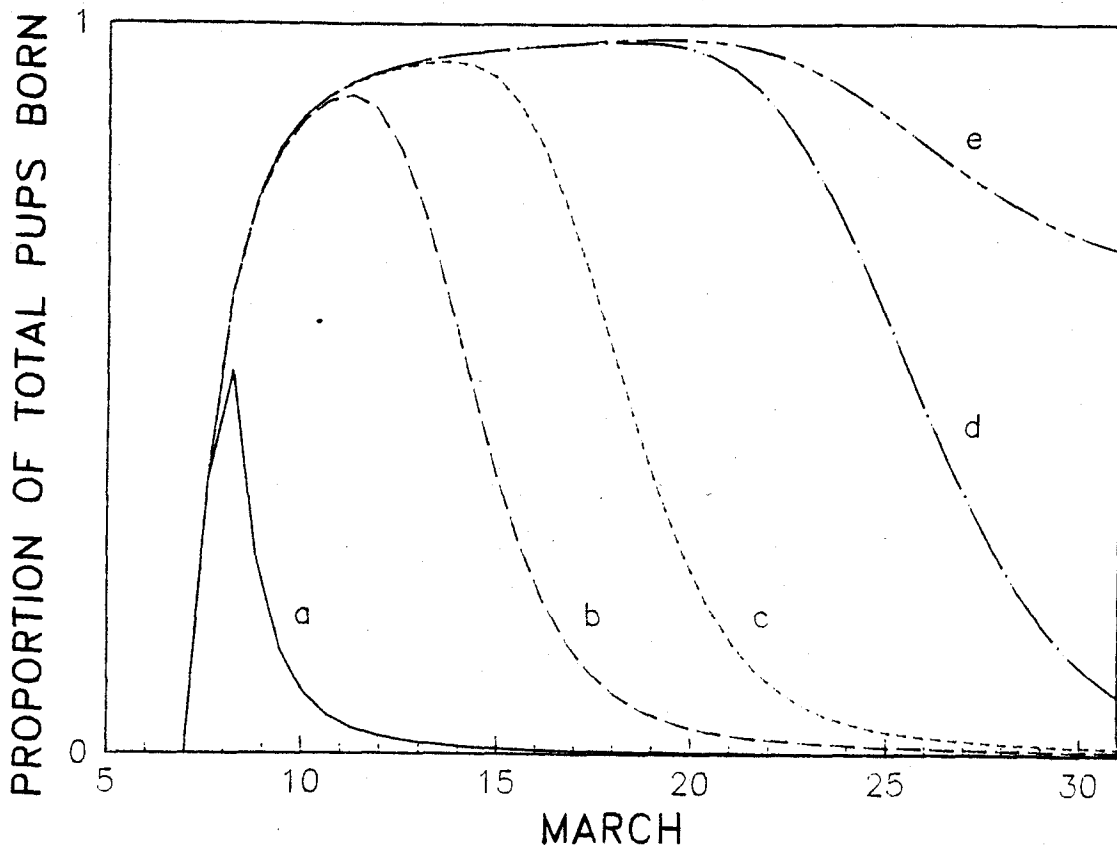


Fig. 3a. Predicted proportion of the total pup production in the main patch in each stage under the assumption of model 1. [a. (—) newborn and yellow pups; b. (-·-) newborn, yellow, and thin white pups; c. (----) newborn, yellow, thin, and fat white pups; d. (-·-·) newborn, yellow, white, and grey pups; e. (····) newborn, yellow, white, grey, and ragged jacket pups.]

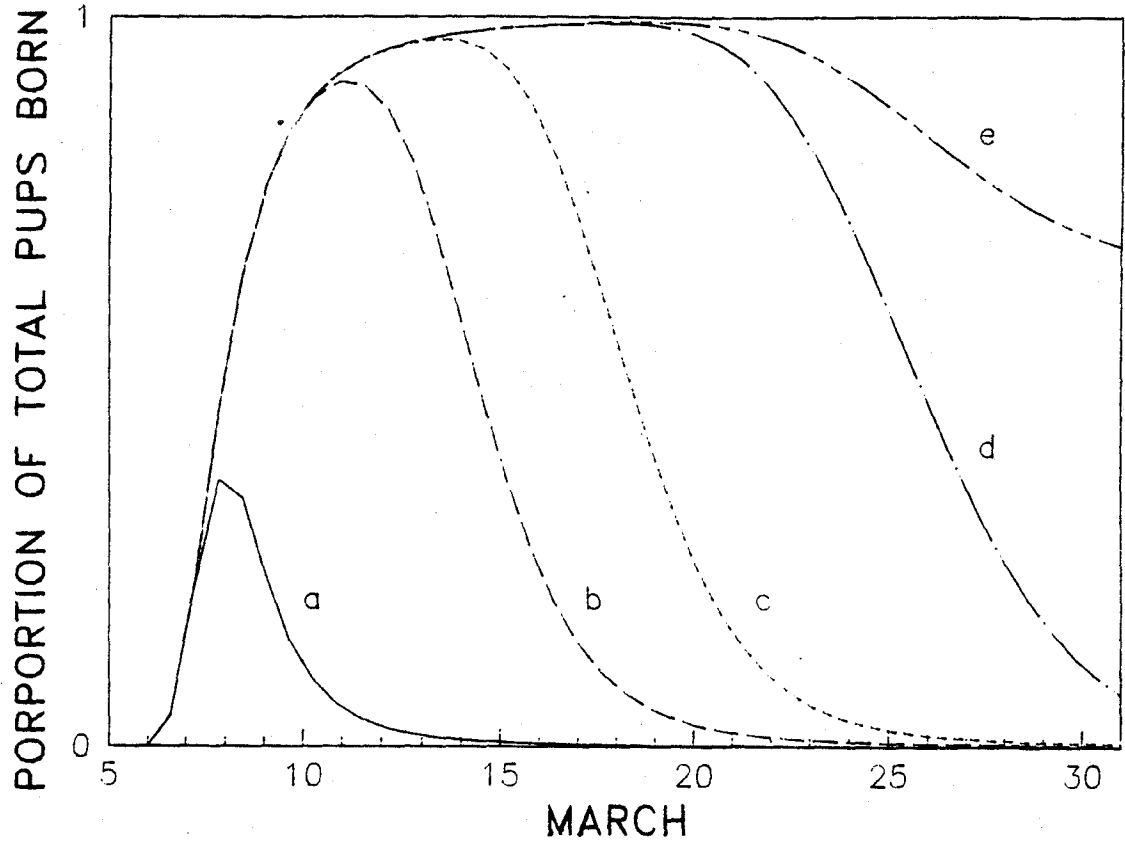


Fig. 3b. Same as Fig. 3a assuming model 2.

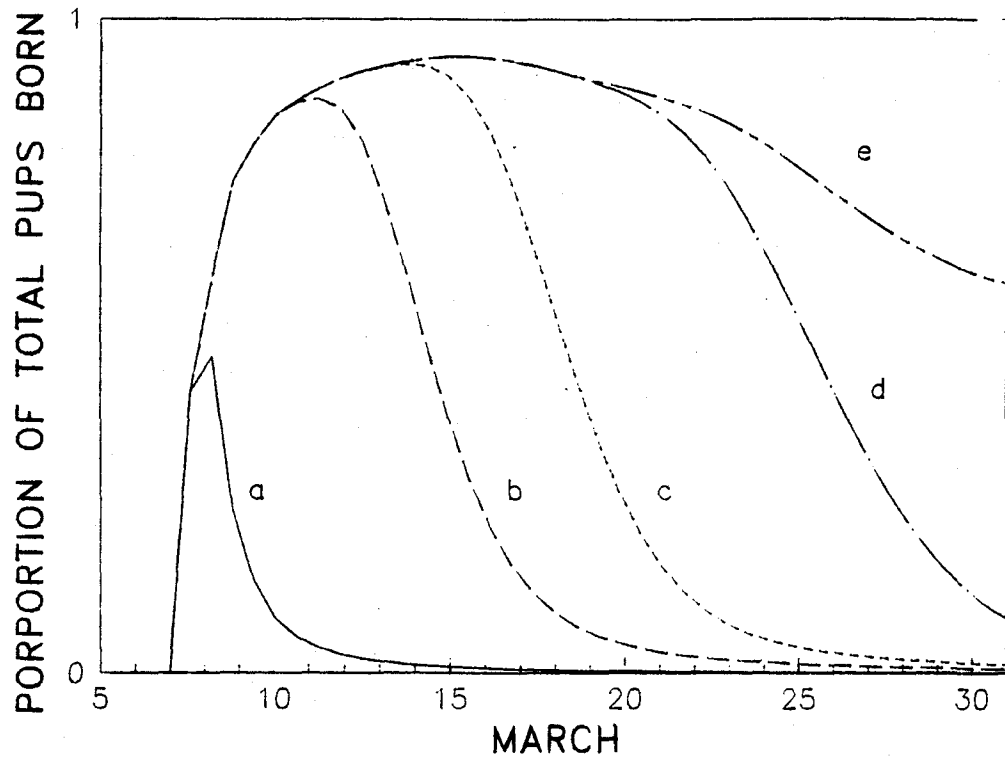


Fig. 3c. Same as Fig. 3a assuming model 3.

Appendix 1. Readings of 10 experimental photographs before and after the reading of the survey photographs (at two grid sizes).

Photo number	4 x 4 grid, pre-survey					8 x 8 grid, pre-survey					8 x 8 grid, post-survey				
	1	37	42	43	38	42	40	46	46	49	48	52	55	53	51
2	33	49	59	60	62	62	67	68	73	73	89	90	88	86	90
3	69	80	80	75	75	78	77	77	74	78	104	106	106	104	105
4	39	40	37	32	33	34	35	35	34	38	49	51	48	48	51
5	105	107	105	106	105	105	108	109	109	114	148	153	150	148	105
6	48	56	56	54	54	61	55	58	59	62	72	77	71	74	73
7	28	36	40	38	42	43	43	49	48	43	55	57	58	57	55
8	26	25	27	25	26	27	27	31	31	34	54	62	60	60	59
9	58	54	58	57	54	61	61	63	61	62	89	85	87	80	85
10	59	65	63	59	61	60	63	67	65	64	80	83	80	82	84
Column sums	50.2	55.4	56.8	54.4	55.4	57.1	58.2	60.2	60.3	61.6	79.2	81.9	80.1	79.0	80.6